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THE SOCIAL LIFE OF ANIMALS

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THE SOCIAL LIFE OF ANIMALS

BY W. C. ALLEE

PROFESSOR OF ZOOLOGY
THE UNIVERSITY OF CHICAGO

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This book is gratefully dedicated to the past and present members of our "Ecology Group"; without their enthusiastic co-operation much of the underlying evidence could not have been collected during my lifetime, and without their critical attention the expression of these ideas would have been more faulty.

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Foreword

I WAS recently honored by an invitation to give the Norman Wait Harris lectures at Northwestern University; the more so since as one of their side-door neighbors I live close enough for my personal foibles to be well known, thereby removing the chief source of any possible glamour. In this book which grew out of those lectures, as in the lecture series itself, I make no effort to pose as the remote purveyor of a mysterious erudition; I could not in any case regard myself as more than the exponent of the glorified common sense which I more and more firmly believe all science should be.

Even more than most, this book is the outgrowth of years of co-operative effort. Some of the basic facts were collected with the aid of funds from the Rockefeller Foundation given to aid biological research at the University of Chicago. Other researches were supported directly by that university and more recently by a grant for the study of the effect of hormones on behavior from the National Research Council.

In addition to the personal aid received from my scientific associates, many of whom will be named in the text, the kindly criticism of Professor Alfred E. Emerson has been particularly helpful in developing the work and in shaping the content and implications of these lectures. My thanks are given also to Professor Sewall Wright for his criticism of Chapter IV, to Mr. Kenji Toda for preparing the illustrations and to Marjorie Hill Allee, whose command of the written word has been a constant resource.

W. C. Allee

The University of Chicago.

I. Science versus Metaphysics

THE RATE of obsolescence of material things is high. With consumers' goods we are well aware of this fact; and even capital goods usually become out of date in a long generation. Last summer an admirer of Will Rogers dedicated a lasting monument to the humorist. Although built for time and erected in our semi-arid West where decay is slow, the tower is expected to last only a thousand years. Invested capital evaporates even with watchful care; there are few private collections of material wealth that remain intact a third of a thousand years.

Oddly enough, the most permanent contributions of our age appear to be the scientific discoveries we have made, the artistic beauties we have created, and the ideas we have evolved. To the extent that these advances are entombed in libraries and museums they share the impermanence of more material things. A nearer approach to immortality is permitted those bits of science and art that escape from the bindings of books and pass into the active life

and traditions of people. The more widespread and firmly fixed these become in the minds of living men, the greater is their chance of longevity.

The most practical achievement of our extremely practical period is the habit of searching for new truths and for correct interpretations of those long known. The unique contribution of the present era is not that made by men of business and affairs, spectacular as it may be. Rather this age is and will be known as the time of the development and application of scientific methods. These contributions are being made by extremely impractical research workers who are supported by a tiny splinter from the great block of capital gains. Money spent effectively to this end, whether in the aid of research or other creative scholarship, or in teaching the results gained by research, makes the most lasting and important of all modern investments. The most nearly permanent monument any man can erect is to have influenced directly or indirectly the growth of improved ideas and traditions among the men in the street, in the factory or on the farm.

It is in this spirit that I have undertaken to interpret one of the significant biological developments of recent years. It is my hope that from the work described in these pages, all social action may have a somewhat broader and more intelligent foundation.

We can gain the impression from some modern oversimplifications that science deals with empirical facts, that philosophy attends to principles and eternal truths, and that religion is concerned with values. In the following pages it will be necessary to shake aside such artificial limits and to present principles along with the evidence that supports them; to test these against experience and to attempt frequently to weigh the general biological values involved. This last process will be easier if we assay survival values only. Admittedly in dealing even with survival values we must be relatively rough and ready in our methods, and perhaps the conclusions will carry a strong odor of the laboratory in which they had their origin.

Basically the approach will be that of the experimental biologist rather than that of the theorist, which might be more polished, or of the philosopher, which would certainly be more abstract and would probably use a great many more words for the same number of ideas. Despite much practice to the contrary, any biological fact which concerns us can be accurately described and the conclusions from its study be clearly expressed in relatively simple and direct language.

In research reports and scholarly discussions there is need for the conciseness and precision made pos-

sible by technical language. Science has no need, however, and is ill-served by any tendency to develop a cult of obscurity. Scientists must be free to attack the unknown as effectively as they can and in return for intellectual freedom they have an obligation, which rests heavily on those able to do so, to interpret research results in terms which can be understood by intelligent and interested people.

There is current in at least one American university at present an attempt to organize all knowledge about metaphysics, and so secure a longed-for unity. In order to obtain a simplified system, the group of men occupied with this enterprise turn back to the days before the present scientific era to find a statement of eternal principles which will serve as a unifying nucleus for human experience and thought. Such efforts at establishing a Neo-Scholastic philosophy, while furnishing an excellent corrective for overconfident scientists, seem mischievously naïve as a serious, present-day movement. We do need relief from our absorbed attention to conflicting scientific detail, but progress must needs come from newer syntheses which take account of the world and man as science sees them rather than by accepting almost as a whole some ancient system of historical significance. These systems are out of date primarily because they were evolved before

one of the greatest advances in knowledge that man has yet been able to make, that of modern science.

Modern philosophical educational systems, if they are to survive, must have as their central core the well-tested evidence compiled by objective scientific methods. Such knowledge must have stood the test of being checked and re-checked by men constitutionally agnostic in their mental attitudes; who can say, "I don't know. What is the evidence?"; who are constantly seeking critical new evidence concerning the validity of their ideas.

An anecdote that is becoming classic among scientists will illustrate the point. Professor Wood, physicist of Johns Hopkins, was asked to respond to the toast "Physics and Metaphysics" at a dinner of some philosophical society. His response was somewhat as follows:

The physicist gets an idea which seems to him to be good. The more he mulls over it the better the idea appears. He goes to the library and reads on the subject and the more he reads the more truth he can see in his idea. Finally he devises an experimental test and goes to his laboratory to apply it. As a result of long and careful experimental checking he discards the idea as worthless. "Unfortunately," Professor Wood is said to have concluded, "the metaphysician has no laboratory."

II. History and Natural History

LIKE other human disciplines, science has its orthodox and its heterodox views. The idea that unconscious automatic co-operation exists has had a long history, and yet it is just now beginning to escape from the heterodox category.

My own interest in this subject dates not from a preconceived idea but from a clearly remembered bump against some stubborn experiments. Almost thirty years ago as a graduate student in zoology I was engaged in studying the behavior of some common small fresh-water animals called isopods, tiny relatives of the crayfish. All fall and winter I had been collecting them from quiet mud-bottomed ponds, chopping the ice if necessary, and from beneath stones and under leaves in clear small streams.

I kept them in the laboratory under conditions which resembled those in which they lived in nature. Then day after day I put lots of five or ten isopods into shallow water in a round pan that had a sanded wax bottom so prepared that the isopods

could crawl about readily. When a current was stirred in the water the isopods from the streams usually headed against it; but those from ponds were more likely to head down current, or to be indifferent in their reaction to the current. The behavior of the two types was sufficiently different so that at first I thought that stream and pond isopods represented different species, but the specialist at the National Museum assured me that all belonged to the species appropriately called *Asellus communis,* the commonest isopod of our inland waters.

Rather cockily I reported after a time to my instructor that I had gained control of the reaction of these animals to a water current. By the judicious use of oxygen in the water, I could send the indifferent pond isopods hauling themselves upstream, or I could reduce the stream isopods to going with the current. I had not reckoned with another factor that presently caught up with me.

After a winter in the laboratory it seemed wise as well as pleasant to take my pan out to a comfortable streamside one sunny April day, and there check the behavior of freshly collected isopods in water dipped from the brook in which they had been living. To my surprise, the stream isopods, whose fellows all winter had gone against the current, now went steadily downstream or cut across it at any angle to

reach another near-by isopod. When I used five or ten individuals at a time, as I had done in the laboratory, they piled together in small close clusters that rolled over and over in the gentle current. Only by testing them singly could I get away from this group behavior and obtain a response to the current; and even this reaction was disconcertingly erratic.

It took another year of hard work to get this contradictory behavior even approximately untangled; (1) * to find under what conditions the attraction of the group is automatically more impelling than keeping footing in the stream; and that was only the beginning of the road that I have kept from that April day to this time, continuing to be increasingly absorbed in the problems of group behavior and other mass reactions, not only of isopods, but of all kinds of animals.

As the years have gone on, aided by student and other collaborators and by the work of independent investigators, I have tried to explore experimentally the implications of group actions of animals. And necessarily, too, I have had to turn to the world's literature to find what others have done and are doing along this line.

* Detailed citations to more complete statements will be found in the bibliography.

A Greek philosopher named Empedocles seems to have had the first recorded glimmerings of an idea of the universal and fundamental nature of co-operation which underlies group action, as well as a conception of the opposing principle of the struggle for existence. Empedocles lived in the fifth century B.C., and he was not only a thinker but so much a man of affairs that he was offered a king's crown, which he refused. (128)

He owes his present-day fame to two long poems in which he outlined the idea that there are natural elements: fire, earth, air, and water, which are acted upon by the combining power of love and the disrupting power of hate. Under the guidance of the building force of love the separate elements came together and formed the world. Separate parts of plants and various unassorted pieces of animals arose from the earth. These, Empedocles taught, were often combined and at first the results were monstrous shapes, which in time became straightened around until, still guided by combining love, they clicked, to make the more perfect animals we now know. It has taken us almost two and a half millennia to transmute this poetic conception into the less picturesque but more exact and workable expression acceptable to modern science.

After the fertile Greek era there intervened in this

field as elsewhere the long sterile period when Greek philosophy, if known, was dogmatically accepted, and shared with other authoritarian systems the responsibility of explaining the world of reality as well as the universe of fancy.

It was not until my own experiments and thinking and reading had begun to form in my mind a fairly definite pattern that, by the aid of Havelock Ellis's *The Dance of Life* (43) I stumbled upon the ideas of the third Earl of Shaftesbury, who lived before and after 1700. He seems to have been the first intellectual in the modern period to recognize fairly clearly that nature presents a racial impulse that has regard for others, as well as a drive for individual self-preservation; that, in fact, there are racial drives that go beyond personal advantage, and can only be explained by their advantage to the group.

An unfriendly contemporary wrote pretty much these words: "Shaftesbury seems to require and expect goodness in his species as we do a sweet taste in grapes and China oranges, of which, if any are sour, we boldly proclaim that they are not come to their accustomed perfection." Havelock Ellis, in reviewing this development, says that "therewith 'goodness' was seen practically for the first time in the modern period to be as 'natural' as the sweetness of ripe fruit." It is only fair to record that in the religious

world for at least fifty years previous there had been growing a similar conviction among certain heretics.

In 1930, after having written the text of a careful account of experimental evidence concerning the existence and non-existence of co-operation at subsocial levels, (3) I set down in the draft of a proposed preface that the existence of such a principle was now for the first time an established fact, for which the details to follow gave full proof. I still think that the proof is good. However, the preface as published does not contain any such claim, for at that point in the writing I went back and re-read *Des sociétés animales* by the French scientist Espinas, (44) which appeared in 1878 and which was the pioneering essay in this field so far as modern work is concerned. There I found Espinas affirming that no living being is solitary, but that from the lowest to the highest each is normally immersed in some sort of social life, a fact which he proclaimed sixty years ago, and added that he was ready to offer conclusive proof.

I turned through the pages past his detailed history of the evolution of ideas about the origin and development of society, and read his massed evidence that communal life is not "a restricted accidental condition found only among such privileged

species as bees, ants, beavers and men, but is in fact universal."

The evidence was largely based on observations of the existence of animal groupings in nature, which are found widely distributed in the different levels of the animal kingdom—facts such as I shall review later in this chapter. It was clear to me that the facts which Espinas had found so impressive had not convinced others and, while suggestive, did not seem compelling to me in the light of other indications to the contrary. Perhaps, I cautioned myself, even the experimental evidence that I had accumulated in 1930 was not really crucial, and it would be well to avoid making too strong a claim in the matter. The same caution must continue even in the face of still stronger evidence known today.

The conclusions of Espinas coming in 1878 are the more important because the scientific world was then, as men in the street are today, under the spell of the idea that there is an intense and frequently very personal struggle for existence so important and far reaching as to leave no room for so-called softer philosophies. The idea of the existence of natural co-operation was apparently in the air despite the preoccupation with this phase of Darwinism. Kessler is said to have addressed a Russian congress of naturalists on this subject in 1880, and from this ad-

dress sprang the remarkable if uncritical book by the Russian anarchist, Prince Kropotkin, on mutual aid. (74)

By combing the accumulated natural history records, Kropotkin was able to collect observation after observation which indicated that animals in nature do aid each other to live, as well as, on occasion, kill each other off. Kropotkin's work served the admirable purpose of keeping this idea alive and popularizing it. It has had also the less fortunate result of bringing Kropotkin's fundamental doctrine into disrepute among students who are critically sensitive to the value of evidence, and who find that Kropotkin's sources were not always reliable.

William Patten, an American biologist who taught for many years at Dartmouth College, made the next general statement of the fundamental nature of co-operation when in 1920 he gave it a central place in his analysis of the grand strategy of evolution. (90) It is of personal interest to me that at the scientific meetings in 1919 at which I presented my first experimental results on this subject, Professor Patten gave a vice-presidential address in which he outlined, mainly from philosophical considerations, his conclusions concerning the importance of biological co-operation. He was rightly impressed by the fact that cells originally were separate, as protozoans are

today. Some, however, evolved the habit of remaining attached together after division. This made a beginning from which the many-celled higher animals could develop. With each increase in the ability of cells to co-operate together there came power to increase the complexity of organization of the cell masses. The highly evolved bodies of men and of insects are thus an expression of increasing intercellular co-operation which finally reaches a point at which, for many purposes, the individual person becomes the unit rather than the co-operating cells of which he is composed.

About the same time the German, Deegener, (40) published an extensive treatise on the social life of animals, along the same lines as the book written by Espinas forty years before. Deegener's distinctive contribution was a classification of the different social levels, from the simplest sorts of artificial collections of animals to parasitism and truly social life. His rating of these different aspects of sub-social and social life in one long outline has the great merit of showing that there are no hard and fast lines which can be drawn between social and sub-social organisms, but that social communities are the natural outgrowth of sub-social groupings. Unfortunately, with Teutonic vigor and vocabulary, he designated the different categories in words as

unwieldy as they were exact. Bogged down by the weight of such terms as *sympatrogynopaedium, synaporium* and *heterosymphagopaedium,* Deegener's real contribution tends to be lost even to biological scholars.

A survey such as I am attempting here should not try to be exhaustive; I shall dismiss with a word the slight advance made by Alverdes (16) and the work of many others without that. There is, however, another phase of the literature whose reading has given me so much pleasure as well as useful information that I shall not pass it over: this deals with the social insects. Espinas, Kropotkin, Deegener and Alverdes of those mentioned, and a host of others, have written in detail and in general about these fascinating insects, but none more accurately or with greater insight and literary as well as scientific skill than the American entomologist, William Morton Wheeler. His book on *Social Life Among the Insects,* which appeared in 1923, is a noteworthy general summary. (120) In this he shows that among insects alone, and including such well-known forms as termites, bees, wasps and ants, and the less generally known social beetles, the social habit has arisen some twenty-four distinct times in about one-fifth of the known major divisions of insects. It would seem that there is a general reservoir of pre-

social traits from which, given the proper opportunity, society readily emerges. Wheeler, no less than Espinas, from whom he quotes, emphasizes that even so-called solitary species of animals are of necessity more or less co-operative members of associations of animals and that animals not only compete among themselves but they also co-operate with each other to secure mates and insure greater safety.

It did not, however, make for the full acceptance of these ideas that Wheeler drew his illustrative material primarily from, and based his conclusions mainly on, his knowledge of social life among insects. The existence of co-operation among nest mates in ants and bees does not prove that there are beginnings of co-operative processes among amoebae and other greatly generalized animals.

Man and the few species of highly social insects are a small part of the animal kingdom; in order to discover and distinguish the principles of general sociology it is necessary to look farther, to focus attention on the social and anti-social relationships of many animals usually regarded as lacking social life.

With and without this end in view there have been in the last twenty years simultaneous but independent outbreaks of experimentation on group effects among the lower animals. For a time just

preceding and following 1920 we, who in Australia, (107) in France (26) and in the United States (2) were engaged in these studies, continued unaware of each other's work. Relatively soon, however, since biological world literature is today widely and promptly circulated, all such work, even that in Russia, (53) became generally known. It is these general experiments on population growth, on mass physiology and on animal aggregations, that are now the important aspect of the field of animal co-operation.

I have briefly traced here the history of the idea of innate co-operation. One reason for the slowness of accepting that idea is the obvious fact that co-operation is not always plain to the eye, and that competition in its most non-co-operative form, in which no social values are apparent, can readily be observed. With certain exceptions to be mentioned soon, it has seemed that, social species aside, crowding, the simplest start toward social life which is easily apparent and a condition of nearly all society, was harmful alike to the individual and to the race. It has been known from experimental evidence since 1854 (62) that crowded animals may not grow at all, or, at any rate, grow less rapidly than their uncrowded brothers and sisters. And under many conditions crowded animals not only do not grow,

they die more readily, and frequently they reproduce less rapidly than if living in uncrowded populations.

All the older works in natural history taught fairly clearly that crowded groups, to have real survival values, must be sufficiently well organized to contribute to group safety by warning of danger or by defense in case of attack. (3) If, in addition, these groups are organized on a basis of division of labor, such as occurs in the highly social colonies of ants or termites, with specialized reproductives, workers and soldiers, or according to the patterns found in human society, then the survival values of groups are readily seen.

Yet for some reason, under natural conditions and with very many sorts of animals, crowding in all degrees does occur and apparently always has occurred. Conceded that animals do not always act for their own best interests, still they must do so to a certain degree or be exterminated in the long run. The advantages of the long-established habit of a species may not be obviously apparent, but it is not safe to say offhand that advantages do not exist.

There are the dense crowds of certain animals, ladybird beetles (Plate Ia), for example, that with the approach of winter collect in restricted and favorable places where they hibernate together. Ap-

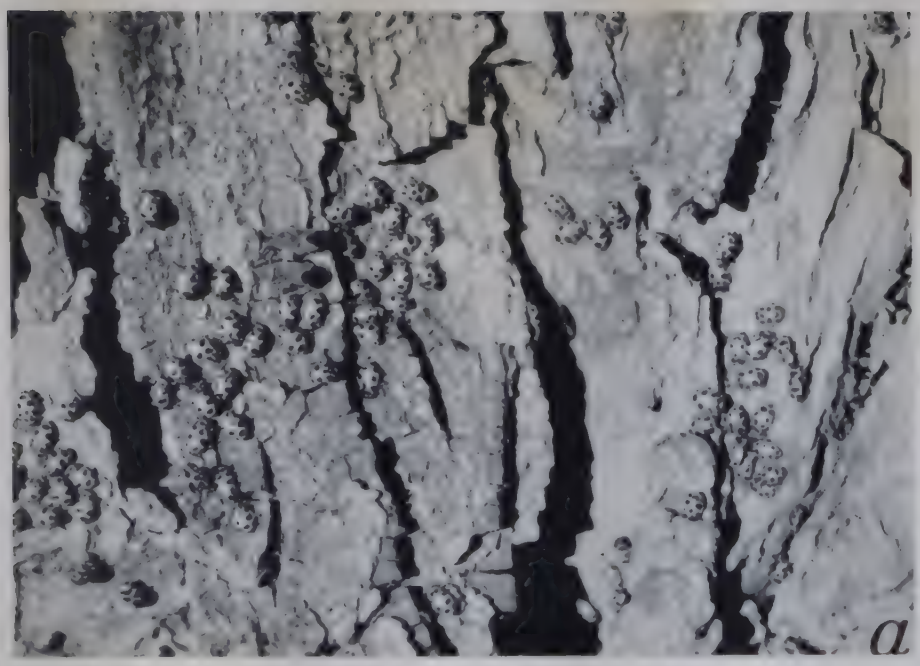


PLATE I. *a*. Ladybird beetles collect in dense aggregations in the autumn and hibernate. *b*. During their breeding season, male midges gather in swarms and await the coming of the females. (Photographs by Welty.)

parently, in the face of winter cold, there is some safety in numbers even among cold-blooded animals that collect in hordes without any organization.

A second plain exception to the general testimony that crowding of non-social species is harmful are the aggregations that form during the breeding season. Like the hibernating groups, these are very widely distributed through the animal kingdom. Breeding aggregations of worms, crustaceans, fishes, frogs, snakes, birds and mammals or the midge insects shown in Plate Ib, for example, have long attracted attention. Their numbers have been great enough and conspicuous enough to stimulate repeated descriptions by naturalists.

A third exception is found during times of migration, when animals frequently crowd together in great hordes and execute mass migratory movements, like those of many birds.

However, breeding, hibernation and migration aside, the older information indicated that up until the point that social life is developed, crowding is harmful.

But there are many other instances of crowding which do not fall under any of these classifications; and it will be worth while to consider here the extent and the natural history of some of these dense animal aggregations. Here, as elsewhere, there will

be no attempt to catalogue all known instances or to select merely the very best cases known. I shall try to use examples that are not too shopworn by repeated description.

Almost every observant person has seen the soft green "bloom" which covers many stagnant ponds. Under the microscope this "bloom" is often seen to be composed of myriads of the tiny plant-animal *Euglena*. These organisms are commonly one-tenth of a millimeter long, which means that in a characteristic layer of "bloom" there would be at least sixty to one hundred thousand animals per square inch; and acres of water are sometimes covered.

Lobster-krills are small crustaceans that occur commonly in shoals about the Falkland Islands, Patagonia, New Zealand and other southern waters. (81) A larval stage of this animal, less than an inch long, occurs often on the surface of the water in such numbers that the sea is red for acres; and whales in those waters simply open their mouths and swim through slowly, feeding with no more effort than the process of straining them out. These shrimp-like animals may be piled up on the shore by tide and wind in stench-producing layers. Dampier wrote of them in 1700: "We saw great sholes of small lobsters, which colored the sea red in spots for a mile in compass"; and they have been known to extend

along the Patagonian coast for as much as three hundred miles.

At Woods Hole, on Cape Cod, I have at certain seasons dipped up a bucket of sea water from the harbor and found more space occupied by clear, jelly-like ctenophores, each the size of a walnut, than was taken by water. Sometimes I have dipped up a fingerbowl of sea water and found it so filled with small pin-point-like copepods that again there seemed to be more of them than of the water itself. These tiny relatives of the lobster-krills are also the food of whales, and they, too, may discolor the ocean for miles.

Around bodies of fresh water, may-flies or midges may emerge in clouds. At Put-in-Bay, near the lights flooding the monument that commemorates Perry's victory, I have picked up living may-flies by the double handfuls from the millions that fly toward the lights; and near by our lake boat steamed through windrows of cast skins of the emerging may-fly nymphs. Nearer Chicago I have taken water isopods, the half-inch crustaceans mentioned earlier, by the bucketfuls from pools where they had collected in numbers only to be compared with those in twenty swarms of bees.

We have already spoken of the migratory hordes. Locusts in migration (116) swarm out of the sky in

the Sahara borderlands, in southern Russia, in South Africa and on the Malay Peninsula in terrorizing numbers (Figure 1). They once did so on the Great Plains of the United States, leaving a lively memory of destruction that is still roused by the smaller migrations that may occur there any summer

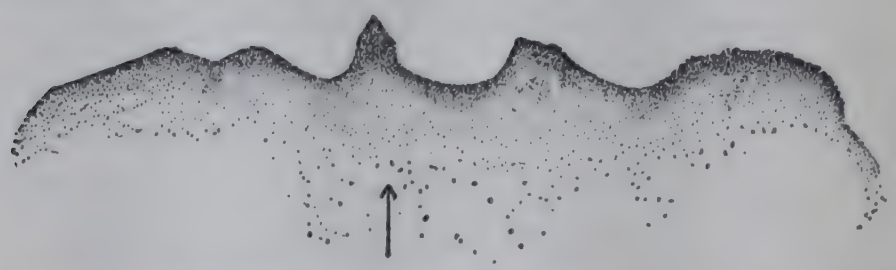


FIG. 1. A band of grasshopper nymphs on the march. (From Uvarov, by permission of the Imperial Bureau of Entomology.)

in spite of active control measures. I myself have seen the so-called Mormon cricket advancing from the relatively barren mountain pastures of Utah into the green fields in numbers which were not halted by the hawks, turkeys and snakes attendant on the swarm and feeding greedily; or the active assaults of men and children warned out to protect the cultivated lands. Migrating army worms and chinch bugs present equally impressive aggregations.

The emergence of Mexican free-tailed bats from the Carlsbad cave of an August evening has been described as a black cloud pouring out in such density as to be visible two miles away. (19) Such bats

are estimated to hibernate in these caves by the millions; and they may be found through the day in sleeping masses a yard across, hanging from the roof like a swarm of bees.

Even larger mammals may collect into great, closely packed herds. The migrating caribou on the tundra are said to pour south in hordes that flow past a given point for hours or even for days. And of the antelope on the plains of Mongolia, (17) Roy Chapman Andrews says that he has seen thousands upon thousands of bucks, does, and fawns pour over the rim and spread out on the plain. Sometimes a thousand, more or less, would dash away from the herd, only to stop abruptly and feed. The mass of antelope were in constant motion even when the animals were undisturbed. They scattered before his automobile only to re-form within a few hours. In that region only the grassland antelope gathers in such immense herds; the long-tailed desert species never does so, probably because there is not enough food to support them in their more arid dwelling place.

These are merely a few of the more dramatic instances of the collection of great masses of animals in a small space. They are more spectacular but probably less important than are the innumerable smaller aggregations of animals which are frequently

encountered. The small dense crowds of whirligig beetles are a case in point. These occur in widespread abundance on the surface of our inland waters.

The more common condition of less intense crowding does not mean that animals are usually solitary. Rather, the growing weight of evidence indicates that animals are rarely solitary; that they are almost necessarily members of loosely integrated racial and interracial communities, in part woven together by environmental factors, and in part by mutual attraction between the individual members of the different communities, no one of which can be affected without changing all the rest, at least to some slight extent.

Let us take an example. Before the coming of the white man, and even a century ago or less, much of the Great Plains was occupied by what ecologists call a grassland-bison community. (4) Grasses could readily grow in the rich soil, even with the usual summer dry spells and the more severe cyclic drouths that occurred even then. By keeping the grasses fairly closely cropped the bison herds prevented the invasion of herbs and shrubs that might have withstood the severities of the climate but could not make headway against continual grazing (Plate II). In this function the bison were joined by

PLATE II. A grassland-bison community. (Photograph from the National Park Board of Canada.)

a myriad of grasshoppers, crickets, meadow mice and prairie dogs. All these were key-industry animals. In one way or another they converted the grass into meat of different sorts, on which the plains Indians, buffalo wolves, hawks, owls, and prairie chickens fed. If the grass failed, then many of the key-industry herb-eaters and those that in turn fed on them must either starve, migrate into another community where they would be disturbing factors, or change their source of food and thereby disturb the balance in their own community.

It must be pointed out here that the plants of this community cannot be set off as separate from the animals. They divide the available space between them; they constantly interact upon each other and upon their physical environment; except for purposes of formal study or in limited fields, the biologist must consider both as members of a given association.

In such a community the effects of the dominant bison were felt in times of stress by the humblest and least conspicuous grasshopper. In the spring of the year hundreds of square miles normally supported populations of six to ten million insects and other invertebrate animals for every acre of land. As with warmer weather the predatory animals returned to the grasslands, these insects were eaten off

until perhaps a tenth of their number could be found later in the season; with the autumn lushness they increased again, only to fall back to some half-million or so per acre during the winter cold.

Similar communities exist among aquatic forms. In fact one of the first demonstrations of such a community was made for the animals living in and on an oyster-bank. (82) A beautiful and penetrating description of the interrelations that may be found in a small lake was published not long after by the late Professor Forbes (48) of the Illinois Biological Survey, in which he pointed out that minnows competed with bladderwort plants for key-industry organisms; and showed that when a black bass is hooked and taken from the water the triumphant fisherman is breaking, unsensed by him, myriads of meshes which have bound the fish to all of the different forms of lake life.

The existence of these communities is now generally recognized, and in order that they may exist it seems that there must be a far-reaching, even if vague and wholly unconscious, co-operation among all the living creatures of the community. It is to such relationships that Wheeler referred when he said, "Even the so-called solitary species are necessarily more or less co-operative members of groups or associations of animals of different species."

Within these communities aggregations of animals occur for a variety of reasons. Their nature can best be shown by a series of illustrations.

One variety of aggregations is that of colonial forms, in which many different so-called individuals remain through life permanently attached together. In the simplest cases all the individuals are alike. Each possesses a mouth and food-catching tentacles, and each feeds primarily for itself, although food caught by one individual may be shared with others near by. In more complex forms some individuals have the mouths suppressed, and receive all their food from those that do take food. They have become specialized as bearers of batteries of stinging cells; they strike actively when the colony is touched, and their stinging cells explode so effectively as to give protection to the colony. Other individuals in the same colony bear medusa-like heads which break away and swim off, producing eggs and sperm, distributing them as they drift. Here is certainly a division of labor though these colonial animals are never rated as social.

Various modifications of such colonial animals are found particularly among the colonial protozoa, sponges and the coelenterates; they also occur higher in the animal kingdom, even among the lower chordates, the great phylum to which man himself

belongs. It is interesting that animals whose structure forces them to the sort of compulsory mutual aid that automatically follows such structural continuity have never progressed far either in social achievement or in the evolutionary scale. When higher animals, such as the lower chordates, show this development they are usually regarded as degenerate members of their general stock. These colonial animals are seldom dominant elements in the major communities of which they are a part. One comes to the conclusion that the more nearly voluntary such co-operation is, the greater its advantage in social life. It might on the other hand be pointed out that when an animal has achieved social organization and division of labor low in the evolutionary scale, the resulting colonies are so well adapted to their environment that there is not sufficient pressure to cause evolutionary changes.

A second type of aggregation occurs when animals are forced together willy-nilly by the action of wind or tidal currents or waves over which they have no control, and whose effects they cannot resist. Many of the masses which lend color to wide patches of the ocean surface are brought together by temporary or permanent currents. Often animals so distributed are thrown down more or less by chance on types of bottom on which they can develop, and

there, if favorable niches are somewhat rare, dense aggregations may result, like New England coral on a suitably hard bottom, or the animals found on a wharf piling.

These accidental animal groupings may persist only as long as the physical forces which brought them together continue to act. Usually, however, they last somewhat longer, as a result of a slightly positive social inertia which tends to keep animals concentrated in whatever place they happen to be found. If the groupings are to have much permanence this quality of social inertia, the tendency of animals to continue repeating the same action in the same place, must be reinforced by another quality: the social force of toleration for the presence of others in a limited space. The densely packed communities of animals on a wharf piling can persist only if toleration for crowding is well developed.

Other dense collections may be brought about by forced movements of animals in response to some orienting influence in their environment. These oriented, compelled reactions are frequently called tropisms. They are shown by the moths or June beetles or may-flies that collect about lights. Such aggregations are a result of the inherited, internal organization of the animals; and the irresistible attraction of the may-fly to the light is joined with

active toleration for the close proximity of others.

Similarly close aggregations occur as a result of the less spectacular trial and error reactions, in which the animals wander here and there, more or less vaguely stimulated by internal physiological states or external conditions, and so come to collect in favorable locations. Collections of animals about limited sources of food give a good illustration. These, too, may show only the social qualities of inertia and toleration.

A decided advance is made when animals react positively to each other and so actively collect together, not primarily because the location is favorable or through environmental compulsion, but as the result of the beginnings of a social appetite. In early stages of such reactions, the movement together may come primarily because the collection of isopods or earthworms or starfishes are substitutes for missing elements in the environment.

Take, for example, the snake or brittle starfishes of the New England coast. These are rare now along Cape Cod, but before the wasting disease swept away the eel grass they were abundant in favorable localities, but were rarely found close together. I have spent hours peering down through a glass-bottomed bucket here and there and round about in one of these localities, and have not seen more than one

PLATE III. *a*. Brittle starfish aggregate readily when put into a bare vessel of sea water. *b* shows conditions ten minutes after *a* was taken. (Photographs by Welty.)

at a time. And I have spent more hours wielding a sturdy garden rake in swathe after swathe through the short eel grass, very rarely pulling in more than one starfish at a haul.

Yet when a few brittle starfishes are placed in a clean bucket of sea water they clump together like magic (Plate III). In bare laboratory aquaria they remain so clumped for weeks; in fact the aggregations become more compact as time goes on as the animals bring back their extending arms and tuck them into the mass. If, however, the aquaria are dressed up by the introduction of eel grass so that conditions approach those found in nature, the aggregations disperse and the starfishes climb actively about over the blades of the eel grass, feeding on organisms and debris found on their surfaces.

The idea that in clean laboratory dishes these starfishes are substituting each other for the missing eel grass was obvious and easy to test. A kind of artificial eel grass was made of glass rods twisted in various shapes so that they offered a supporting framework for climbing in much the same way as the true eel grass. So long as the rods remained the starfishes clambered about over the meshwork or hung motionless, usually isolated. If the rods were removed they again clustered together.

As I have said elsewhere, (3) it is a far cry from

such aggregations to the groupings of foreigners in a strange city that result in Little Italy, or the Mexican settlement, or a German quarter; and yet basically some of the factors involved are similar. Perhaps there is a closer connection between such aggregations in the wide expanse of a clean aquarium and the schooling tendency found among many fishes of the open sea; perhaps the same phenomenon accounts for the flocking tendency of many birds, as well as mammals on the equally monotonous grassy seas of temperate plains.

A somewhat different expression of a positive social reaction is shown when animals that are usually more or less isolated come together and pass the night grouped as though they were engaged in a slumber party. This type of behavior has been repeatedly described for different insects, even for the wasps that remain separate to such an extent that they are called solitary wasps. In some forms of solitary wasps both males and females are found in the sleeping group. With solitary bees, such as we have near Chicago, the overnight aggregations are composed of males only. A study which was made of the sleeping habits of a Florida butterfly species indicates that these Heliconii (69) come together night after night in the same location, in part at least as a result of place-memory. The assemblages

lack sexual significance. There is some protection in the fact that if one is disturbed the whole group may be warned. The presence of many butterflies would reinforce any species odor that might attract others of the same species, or repel possible predators.

The crowded roosts to which certain birds return not only for one season but sometimes for years are widely known. Here again we are concerned with a positive social appetite which grows stronger with the approach of darkness; the details as to why and how it operates are not known.

Animals which come together in intermittent groupings like these overnight aggregations are showing a social appetite which is none the less real because it is effective only at spaced intervals. In this it resembles other appetites such as those for food, water and sex relations. From such occasional or cyclic expressions of a social appetite it is a relatively short step to whole modes of life which are dominated by a drive for social relationships. As I have already said, in the insects alone this step has been taken some twenty-four distinct times and in widely separated divisions of that immense group.

Normally the development of highly social life comes by way of an extension of sexual and family relations over greater portions of the life span. Here again all degrees of increased length of asso-

ciation can be shown, from the sexual forms that meet but once and for a brief moment to the termite kings and queens that live together for years. Also all stages exist in the evolution of the association of parents with offspring, from the insects like the female walking-stick, which deposits eggs as she moves about and pays no more attention to them, to the ants and bees whose worker offspring spend their entire lives in the parental colony or some colony budding off from it.

While the extension of family relations is very obviously one potent method by which social life is developed to a high level, there are other social groupings which also deserve consideration in connection with the problem as to the method of evolution of social life. Schools of fish arise, for example, under conditions in which there is no association with either parent after the eggs are laid. At times the eggs may be so scattered in the laying that the schools form from unrelated individuals. Here the schooling tendency seems to underlie rather than grow out of family life. The mixed flocks (22) of tropical birds which are composed of many species obviously did not grow directly from family gatherings, and the groups of stags of Scottish deer, probably the original stag parties, (38) appear to give evidence of a grouping tendency independent

of intersexual or family relations. This subject will be discussed in more detail in the final chapter.

The conclusion seems inescapable that the more closely-knit societies arose from some sort of simple aggregation, frequently, but not necessarily, solely of the sexual-familial pattern. Such an evolution could come about most readily with the existence of an underlying pervasive element of unconscious co-operation, or automatic tendency toward mutual aid among animals.

In the simpler aggregations evidence for the presence of such co-operation comes from the demonstration of survival values for the group. These are more impressive the more constant they are found to be. If they exist throughout the year they are much more important as social forerunners than if present only during the mating season or at times of hibernation.

III. Beginnings of Co-operation

WITH this chapter I begin the presentation of the evidence for the assertion that there is a general principle of automatic co-operation which is one of the fundamental biological principles. The simplest expression of this is often found in the beneficial effects of numbers of animals present in a population. Laboratory work of the last two decades still shows that overcrowding is harmful, but it has also uncovered a no less real, though somewhat slighter, set of ill effects of undercrowding.

To be sure, overcrowding always produces ill effects, and these can always be demonstrated at some population density. On the other hand, the ill effects of undercrowding cannot always be shown, though frequently they can. In generalized curves the matter may be summarized thus: Under certain conditions (96) we find the curve running like the diagram in Figure 2A, when height above base line gives the rate of the biological action being measured, and distance to the right shows a steadily in-

creasing population. Under these conditions only the ill effects of overcrowding are visible, and the optimum population is the lowest possible. This is the modern expression of what used to be called the struggle for existence. In the more poetic post-Darwinian days this struggle was thought of as so intense and so personal that an improved fork in a bristle or a sharper claw or an oilier feather might turn the balance toward the favored animal. Now we find the struggle for existence mainly a matter of populations, measured in the long run only, and then by slight shifts in the ratio of births to deaths.

A second type of phenomena is represented by a curve with a hump near the middle (97) as shown in Figure 2 B.

Again, height above the base line measures the speed of some essential biological process or processes, such as longevity; distance to the right gives increasing population densities. The harmful effects of overcrowding, indicated by the long slope to the right, are still plainly evident, but there is also apparent a set of ill effects associated with undercrowding which are shown by the downward slope to the left. Many have written pointedly about overcrowding, and while there is still much to be learned in that field, it is in the recently demonstrated existence of undercrowding, its mechanisms and its im-

plications, that freshness lies. Without for one minute forgetting or minimizing the importance of the right-hand limb of the last curve, it is for the more romantic left-hand slope that I ask your attention.

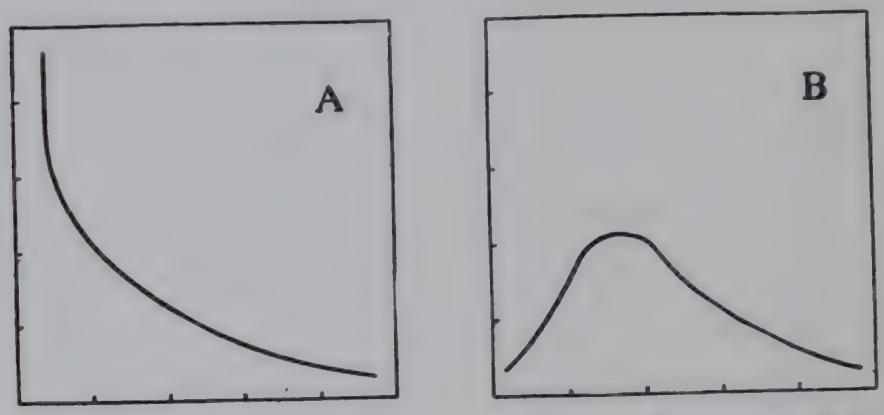


FIG. 2. A. Under some conditions the rate of biological action which is being measured is greatest with the smallest population, and decreases as the numbers increase. B. Under other conditions there is a distinct decrease in the rate of the measured biological reaction with undercrowding (to the left) as well as overcrowding (to the right).

Perhaps the simplest and most direct demonstration of certain harmful effects of undercrowding comes from an experiment which I understand is carried on spontaneously among undergraduate men at certain universities and colleges of which X, or perhaps better, Y, is an example. A certain number of men gather together in a limited space under artificial light and undertake to consume a more or less limited amount of stronger or weaker alcohol. If

there are many men present in proportion to the amount of alcohol, relatively little or no harm will result from the experiment. If there are very few men and much alcohol there may be garage bills and other important repairs to be made.

In one way or another similar tests have been carried out in the laboratory with a variety of poisons, and many kinds of animals. Again I choose from the mass of available evidence the results of a simple and clean-cut experiment to illustrate the same point with non-human animals.

Everyone is acquainted with goldfish; they are hardy forms or else they would not be alive today in so many goldfish bowls. Colloidal silver in its commercial form of argyrol is also well known. Colloidal silver, that is, the finely divided and dispersed suspension of metallic silver, is highly toxic to living things, including even the hardy goldfish.

In the experiment in our laboratory (8) we exposed sets of ten goldfish in one liter of colloidal silver, and at the same time placed sets of ten similar goldfish, one each, in a whole liter of the same strength of the same suspension. This was repeated until we had killed seven lots of ten goldfish and their seventy accompanying but isolated fellows. Then when the results were thrown together we had the simple table on page 54.

TABLE I

Survival in minutes of goldfish in colloidal silver

NUMBER GROUPED	NUMBER ISOLATED	DIFFERENCE	STATISTICAL PROBABILITY
7 × 10	70 × 1		
182 min.	507 min.	325 min.	$P < 0.001$

Any biological experiment has a large number of so-called variables, that is, of factors that it is difficult or impossible to bring under such complete control that we can be certain that the experiment will be exactly repeatable next time. Hence it is customary to make experiments if possible as paired experiments, in which one set of conditions (those of the group in this instance) will differ from another lot (those of the isolated goldfish) only by the one difference, in this case of grouping and isolation. Such results with these fish can then be analyzed by statistical methods to find the probability of getting like results merely "by chance." These methods are now so simple that even I can make the calculations. They are as accepted a technique as is the paired experiment.

With the goldfish there is less than one chance in a thousand of getting as great an average difference with the same number of trials. Technically we say that probability, or P, for short, is less than 0.0001.

It means the same. Students of statistics have found that when $P = 0.05$ or less, that is, when there are fewer than five chances in a hundred of such a thing happening as a result of random sampling or "chance," there is likely to be something significant in such results, the more so the smaller the fraction which P is said to equal.

We make such tests of our experimental results continually, to find how we are getting on, and I shall give probabilities repeatedly. In doing so it must be remembered that these test the data, not the theory—and that the data may vary significantly for unknown reasons, even when we think we are in full control of the situation; and that because there is only one chance in one hundred, or ten thousand, or a million that a thing may happen by "chance" does not mean that it will never happen through what we call an accident; merely that the chances of its happening so, our evidence being what it is, are on the order of one in one hundred, or ten thousand, or a million.

I will digress even further into the realm of coincidence. A Negro friend of mine spent a summer in Europe and while in Paris visited the art galleries of the Louvre. While there he saw a Negro woman busy looking at pictures and on coming closer discovered that she was his own aunt. Neither had any

idea that the other was in Europe. With no prearrangement, what is the probability that an American Negro from Chicago will meet his aunt in the Louvre? Yet it did happen this once without in any way shaking the probability principle.

Perhaps the digression is not so great as might appear at first glance, for we need a slight common understanding of the practical working of statistical probability; all of modern science, the more as well as the less exact, is built on it.

To get back to our goldfish: those in the groups of ten lived decidedly longer than their fellows exposed singly to the same amount of the same poison; and significantly so. But why? Others had made that experiment with smaller animals, and had decided that the group gave off a mutually protective secretion which would protect that particular species and none other. One reason that we were working with goldfish was because they are large enough so that we could use approved methods of chemical analysis in finding where the silver went. The balance sheet from such tests showed that we could account for all the silver present. With the suspensions which had held ten fish the silver was almost all precipitated, while in the beakers that had held but one fish almost all the silver was still suspended.

When exposed to the toxic colloidal silver the

grouped fish shared between them a dose easily fatal for any one of them; the slime they secreted changed much of the silver into a less toxic form. In the experiment as set up the suspension was somewhat too strong for any to survive; with a weaker suspension some or all of the grouped animals would have lived; as it was, the group gained for its members a longer life. In nature, they could have had that many more minutes for rain to have diluted the water or some other disturbance to have cleared up the poison and given the fish a chance for complete recovery.

With other poisons, other mechanisms become effective in supplying group protection. Grouped *Daphnia,* (50) the active water fleas known to all amateur fish culturists, survive longer in over-alkaline solutions than daphnids isolated into the same volume. The reason here is simple. The grouped animals give off more carbon dioxide, and this neutralizes the alkali. Long before the isolated individual can accomplish this, it is dead; in the group those on the outside may succumb, though if the number present is large enough even they may be able to live until the environment is brought under temporary control.

Frequently the protective mechanism is much more complex. With many aquatic animals, other things being equal, isolated animals consume more

oxygen than if two or more share the same amount of liquid. By one device or another, grouping frequently decreases the rate of respiration. Several of these devices are known to us. Professor Child showed many years ago (31) that when animals are exposed to a strongly toxic material, those with the higher rate of respiration, though otherwise similar, die first. This has been applied to group biology by direct tests, and it has been shown that the group, by decreasing the rate of oxygen consumption of its members, makes them more resistant to the action of relatively strong concentrations of toxic materials.

Perhaps I have said enough to show that under a variety of conditions groups of animals may be able to live when isolated individuals would be killed or at least more severely injured by unaccustomed toxic, chemical elements, strange to their normal environment.

Will the same relationship hold in the presence of changes in *physical* conditions? There is a considerable and growing lot of evidence that massed animals, even those that can be called cold-blooded, are harder to kill by temperature changes than are similar forms when isolated. (51, 126) This interests us because massing of such animals at the onset of hibernation was recognized as one of the early ex-

ceptions to the rule, now outgrown, that crowding is always harmful.

The exploration of temperature relations is a time-honored field. I prefer to take up a newer though related area, that of the effects of ultra-violet radiation, in which I shall present some evidence so recently collected that it has never been reported extensively before. A year ago Miss Janet Wilder and I began exposing the common planarian worm of this region to ultra-violet radiation, to find whether there was any group protection from the well-described lethal effect of ultra-violet light on these worms. (12)

In lots of twenty, worms of similar size and the same history were placed together in a petri dish and exposed to the action of the ultra-violet light long enough so that they would disintegrate within the next twelve hours. Half of them, that is, ten worms, were then placed together in five cubic centimeters of water and each of the other ten was put into five cubic centimeters of similar water. Grouped and isolated worms were treated alike in every way, except that after irradiation together, half were grouped and half were isolated.

For one purpose or another we have repeated this simple experiment a great many times with a variety of waters, and with experimental conditions ade-

quately controlled. Some of the things we have found out are:

If the worms are crowded under the ultra-violet lamp so that they shade each other, the shaded ones

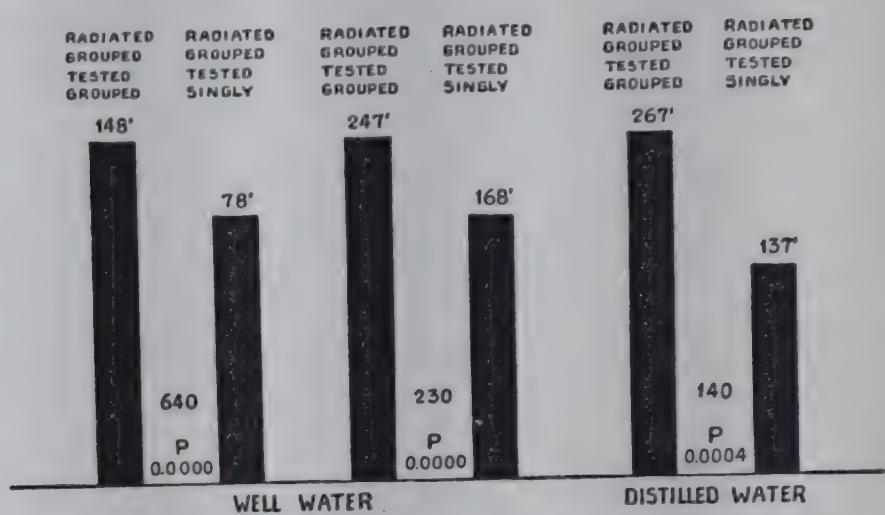


FIG. 3. Planarian worms which have been exposed to ultra-violet radiation disintegrate more rapidly if isolated than if grouped.

are definitely protected. When such crowding is eliminated and by constant watching and stirring, if needed, during exposure, the worms are kept approximately equally spaced, even then the grouped worms survive longer than if isolated. Some of the relationships are shown in Figure 3.

Each block represents the survival time of several series of worms. The figures at the top of the block give the average length of survival in minutes. The blocks are constructed so that the worms surviving

longer, which in each case are the grouped worms, are given as 100 per cent, regardless of the time taken; while the isolated worms, which had been irradiated in the same dishes as their accompanying groups, survived on an average of 78 per cent and 77 per cent respectively in the two tests with well water, and only 61 per cent in the test in distilled water. The numbers between the blocks show the number of worms averaged for each block; that is, the number of pairs of worms for which results are summarized. The statistical significance given in terms of "P" is very high in each case.

The number present during exposure is important, as well as the number present during the time when it is being determined how long the animals will survive. Such data are summarized in Figure 4, which is built exactly on the same principle as that preceding. Worms radiated when crowded (left-hand block), and then tested when isolated, survived 517 minutes, while accompanying worms which had been radiated singly as well as tested when isolated, lived only 24 per cent as long. Those radiated in a group and tested singly (middle block) lived 55 per cent as long as those which had been radiated in a crowd and then were isolated to observe the effects of radiation. It will be remembered that these crowded worms actually shaded each other and so gave

physical protection from the ill effects of ultra-violet light. Finally (on the extreme right) is diagramed the fact that worms radiated and tested singly lived only 62 per cent as long as those radiated in a group

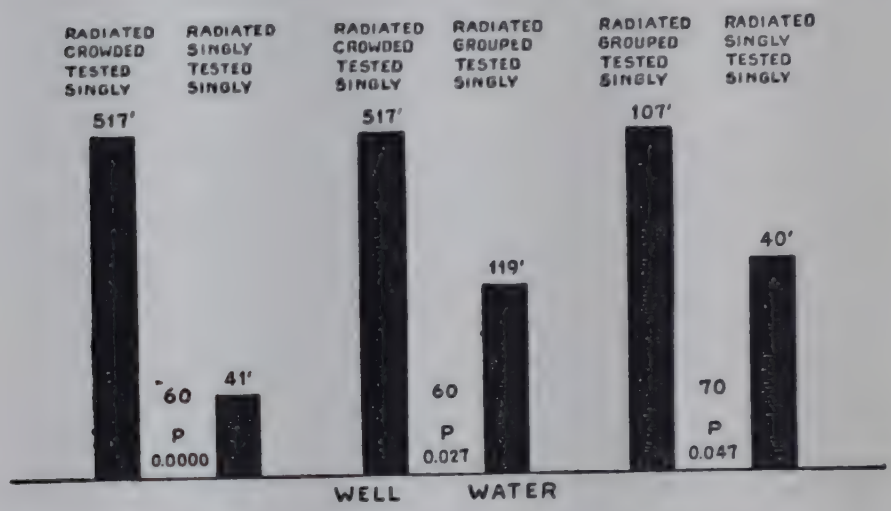


FIG. 4. Planarian worms survive exposure to ultra-violet radiation better if much crowded while being radiated, or even partially crowded, even though all are isolated after a few minutes of irradiation.

of 20 per 20 cubic centimeters and also tested singly. Again the figures give the number of pairs tested and under "P" the statistical probability, which shows that all these must be taken seriously even though there is decreasing significance as the percentage of difference of average survival time decreases.

In the two cases just outlined mass protection has been demonstrated, first against the presence of toxic

materials, and second against the ill effects of exposure to lethal ultra-violet rays. To complete the picture I have now to describe the results of exposing animals to harmful conditions in which the difficulty is caused by the absence of elements normally present in their natural environment. The experiment has been made on aquatic animals in a number of ways, for example, by putting fresh-water animals into distilled water; but it is easier to demonstrate when marine animals are placed in fresh water.

Again I select one experimental case from several available. Near Woods Hole, on Cape Cod, a small flatworm *Procerodes* (Figure 5) lives in certain restricted areas in large numbers. They are most abundant along a stony stretch at about the low tidemark or a little beyond it. (5) There, if one finds the proper location, one may take from ten to fifty flatworms from the lower surface of a single stone. Usually they are more or less clumped together. They are not easy to see since each is only a few millimeters long and all are of a dull gray color. Once seen, they are hard to detach, for the posterior end has a muscular sucker, by means of which the animal can cling pretty securely even to smooth stones. When these worms are put into fresh water, pond water for example, they swell greatly and soon begin to disintegrate.

If these flatworms are washed thoroughly to remove sea water from their surfaces, and then placed in fresh water, a certain proportion of the grouped

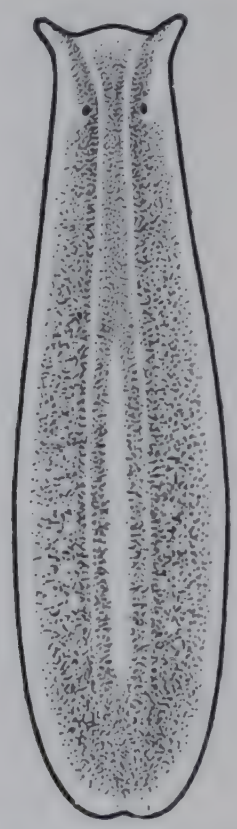


FIG. 5. The small marine flatworm *Procerodes.*

animals survive decidedly longer than isolated worms. The first worms to die in the group do so almost as soon as the first isolated worms. As the dead worm disintegrates it changes the surrounding water; we say it *conditions* it; and as a result of this conditioning the remaining worms of the group have a better chance of life.

For more careful experimentation, a sort of worm soup was prepared by killing a number of well-washed worms and allowing them to remain in the water in which they had died and so condition it. Freshly collected *Procerodes* lived longer in such conditioned water than their fellows which were isolated into uncontaminated, clean pond water. The difference between the two waters was only that caused by the fact that in one the worms had died and disintegrated, while the other was clean. This difference in survival persisted even when, to make the test more revealing, the total amount of salt in the two waters was made identical by adding some dilute sea water to the clean pond water. Results from these experiments are shown in Figure 6. In this chart, distance above the base line gives the percentage of survival, and distance to the right shows time of exposure. It will be noted that the worms lived decidedly longer in the conditioned water than they did in dilute sea water of the same strength of salts.

The mechanism of this superficially mysterious group protection is now known. (86) The dead and disintegrating worms, or more slowly, the living worms, give off calcium into the surrounding water, and calcium has a protective action for marine animals placed in fresh water or for fresh-water animals

put into distilled water, a protective action which is out of all proportion to its effect in increasing the osmotic pressure of the water. We can demonstrate that this is in fact the mechanism of such group

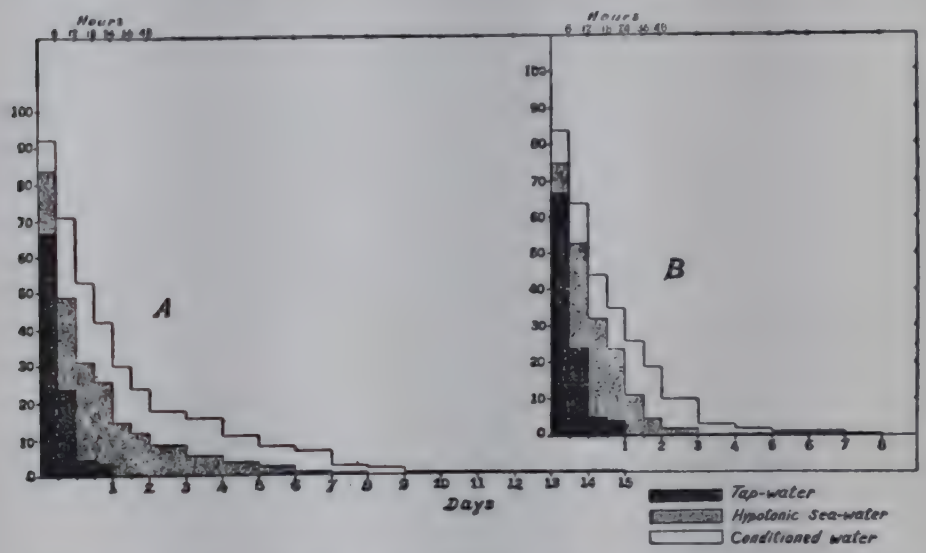


FIG. 6. *Procerodes* die more rapidly if transferred to pure fresh water than in dilute sea water, but live longer if placed in fresh water in which other *Procerodes* worms have died, even though the total amount of salt is the same as in the dilute sea water.

protection. For example, we can analyze the water which worms have conditioned, find the amount of calcium that has been added, and by adding that amount directly get the same results that we do from the conditioned water.

This explanation is not yet complete—no scientific explanation ever is—but we have demonstrated that what was for a time a very mysterious group pro-

tection is in fact in this case an expression of calcium physiology. The further developments on the subject await exact information concerning the details of the physiological effects of calcium.

It is probably of more direct human interest to

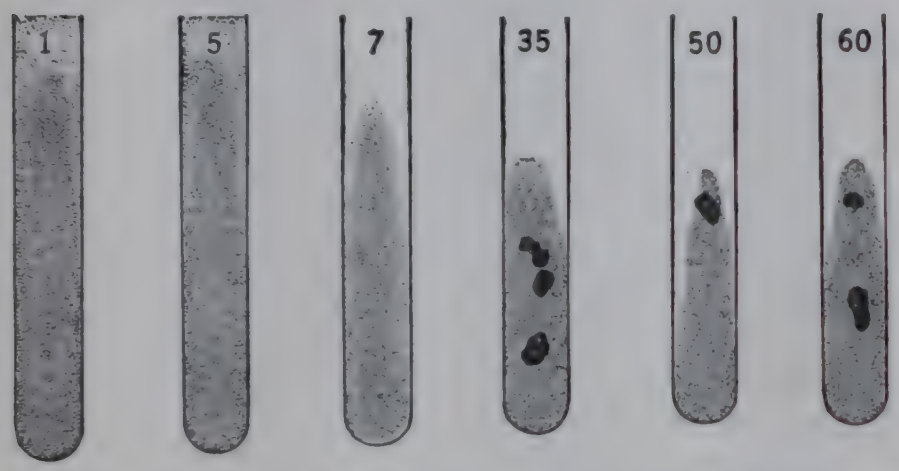


FIG. 7. Bacteria frequently do not grow if inoculated in small numbers; here different numbers of *Bacillus coli* were inoculated into a medium containing gentian violet.

know that under many conditions bacteria will not grow if only a few are inoculated into an animal, man for example; while with a larger inoculation they may grow abundantly. (33) Gentian violet is a poison for many bacteria and in regular medical use for that purpose. In one well-studied case (Figure 7) bacteria belonging to the species *Bacillus coli* failed to grow on agar containing gentian violet, if singly inoculated on it; only when thirty or more bacteria

were inoculated did steady and regular growth occur. With the goldfish spoken of earlier, the mass protection was largely or wholly inoperative when the group of ten was exposed to ten times the amount of toxic colloidal silver to which a single fish was exposed. With these bacteria, however, such quantitative limitations did not hold; thirty organisms were found to fix at least two hundred times the amount of poison normally neutralized by an isolated bacterium. This difference between the change which thirty bacteria can effect together as compared with what they can accomplish if isolated has been called an expression of the communal activity of bacteria. There is a fairly large and growing literature on this subject which indicates that when only one or a few bacteria, even if strongly pathogenic, gain access to the human body, they are likely to be killed by various devices which aid in resisting infection. It is fortunate for their victims that bacterial infections normally tend not to take unless the inoculum is somewhat sizable or unless a smaller dose is frequently repeated.

Mass protection is known to occur among spermatozoa. Many animals, especially those that live in the ocean, shed their eggs and spermatozoa into the sea water, and fertilization takes place in that medium. Dilute suspensions of such spermatozoa lose

their ability to fertilize eggs much sooner than if they are present in greater concentration. It is routine laboratory practice in experimenting with such animals as the common sea-urchin, *Arbacia,* to keep sperm in a cool place, densely massed outside the body, for hours. Small drops can be withdrawn as needed for experimentation, greatly diluted and used almost immediately to fertilize eggs. When such dilute suspensions have long since lost their fertilizing power the sperm in the original dense mass are still potentially as active as ever.

So far we have been considering mass effects, the survival value of which, if any, was shown by increased length of life, often under adverse circumstances. Under many different conditions and for a variety of organisms, the presence of numbers of forms relatively near each other confers protection on a part of those grouped together or even on all present.

It is possible to go a step farther and demonstrate a more actively positive effect of numbers of organisms upon each other when they are collected together. Again I select a fresh case for close scrutiny; that of crowding upon the rate of development in sea-urchin eggs.

Arbacia, mentioned above, is the common sea-urchin of coastal waters south of Cape Cod (Fig-

ure 8). It has been much used in studies of various aspects of development, particularly by the biologists who gather each summer in the research laboratories at Woods Hole, Massachusetts. There are several reasons for its popularity. These urchins are abun-

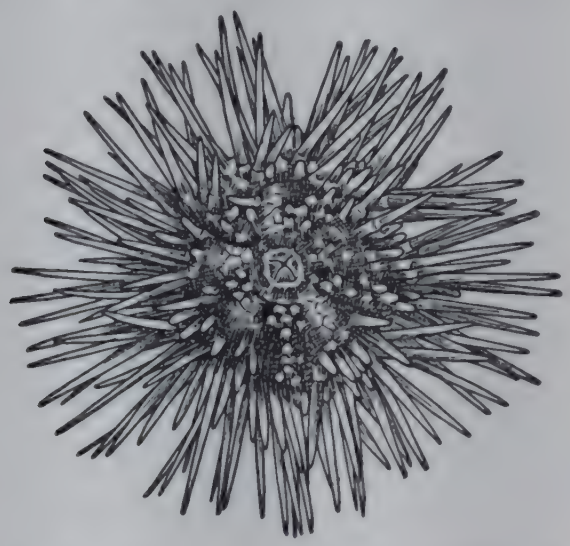


FIG. 8. *Arbacia,* the common sea-urchin of southern New England, shown from the upper surface.

dant in near-by waters and are readily mopped up by the tubful. They can be kept in good condition for some days in the float cages, and eggs and sperm are readily procured as needed. Also the breeding season of *Arbacia* extends through July and August, which are favored months for research at the seaside.

For years biologists at Woods Hole have studied the embryology and physiology of developing sea-urchin eggs. They have built up a painstaking, almost a ritualistic, technique for handling glassware,

towels and instruments. The procedures require as rigid cleanliness as a surgical operation. Consequently it was not surprising when I first took up their study a few years ago, to have one of my frankest friends among the long-time workers on the development of *Arbacia,* voice what was apparently a common feeling among them. He asked pointedly if I thought I could come into that well-worked field and without long training find something they had overlooked. Such frank skepticism was refreshingly stimulating and added to the normal zest of biological prospecting.

The shed eggs of *Arbacia* are about the size of pin points and are just visible to the naked eye. The spermatozoa are tiny things; the individual sperm are invisible without a microscope although readily seen when massed in large numbers. When a few drops of dilute sperm suspension are added to well-washed eggs, one spermatozoan unites with one egg.

After some fifty minutes at usual temperatures, the egg divides into two cells. We call this the first cleavage. Thirty or forty minutes later a second cleavage takes place and thereafter cleavages occur rapidly. Within a day, if all goes well, such an egg will have developed into a freely swimming larva. Other things being equal, (10) the time after fertilization to first, second and third cleavage is speeded

up for the crowded eggs. Typical results and some of the methods are shown in Figure 9. With appro-

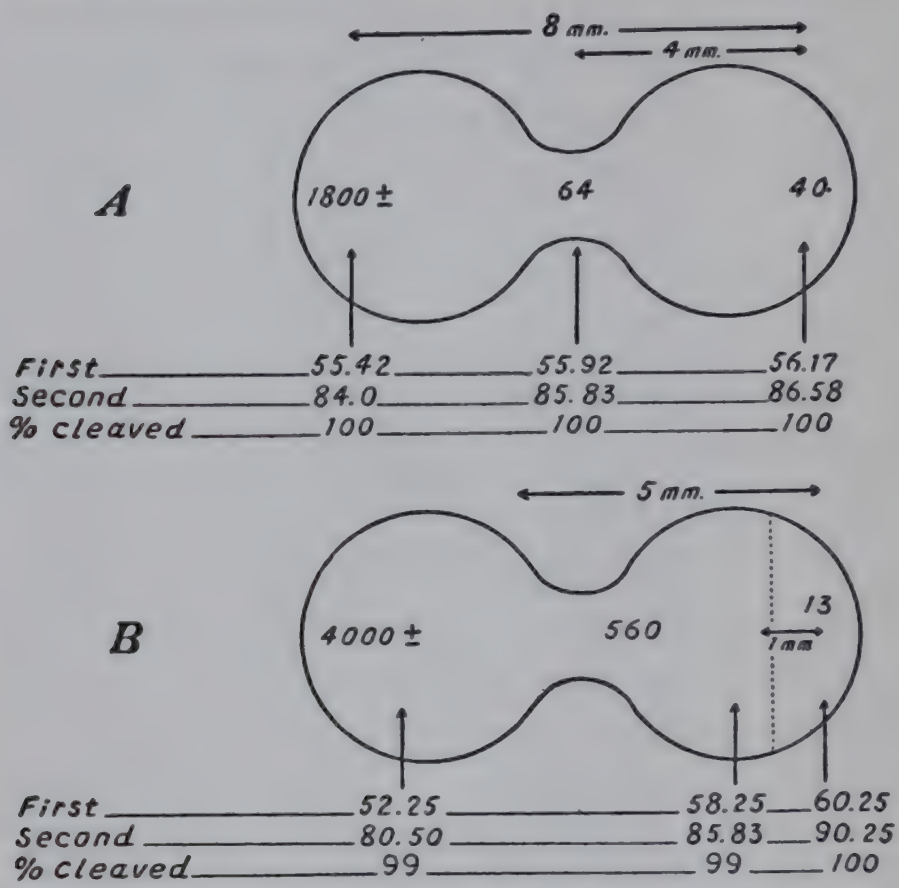


FIG. 9. Eggs of the sea-urchin, *Arbacia,* cleave more rapidly in dense populations than if only a few are present. Figures below the diagrams, unless otherwise indicated, give time in minutes.

priate experimental precautions, some eighteen hundred eggs were introduced into a tiny drop of sea water. Near by on the same slide forty similar eggs were placed in a similar drop and the two were connected by a narrow strait as shown in the figure.

A few eggs from the larger mass spilled over into this strait. The whole slide was placed in a moist chamber to avoid drying, and examined from time to time. In a trifle over fifty-five minutes half the eggs in the densest drop had passed first cleavage. A half-minute later, 50 per cent of those in the strait were cleaved, and twenty seconds later half of the more isolated ones had divided. The time to 50 per cent second cleavage ranged between eighty-four minutes for the crowded eggs and over eighty-six and a half minutes for the isolated ones.

This was repeated with four thousand eggs or thereabouts in the denser population, almost six hundred of which spilled through and formed a flat apron over the bottom of the second drop, in which there were thirteen other eggs scattered singly about the relatively unoccupied space. Under these conditions the time to 50 per cent first cleavage was approximately fifty-two, fifty-eight and sixty minutes respectively, and the difference at the middle of the second cleavage was even greater.

In association with Dr. Gertrude Evans, who is a good, skeptical research worker, this experiment was repeated in many different ways, and there remains in my mind no doubt but that under a variety of conditions the denser clusters of these *Arbacia* eggs

cleave more rapidly than associated but isolated fellows.

Under the conditions tested, the stimulating effect of crowding could be detected when sixty-five or more eggs were present in the more crowded drop and twenty-four or fewer eggs made up the accompanying sparse population.

Within twenty-four hours, under favorable conditions, one finds one's cultures full of free-swimming larvae with characteristic arms which are known as plutei. When all our available data collected the first day after fertilization are compared there is again no doubt but that the more crowded cultures usually develop more rapidly than accompanying but sparser populations. However, it must be recorded that throughout the whole series there were occasional isolated eggs that developed as rapidly as the best of the accompanying denser populations. Such eggs and embryos were exceptional in our experience; the fact that they exist indicates clearly that under the conditions of our experiments crowding, while usually stimulating, was not absolutely necessary for rapid cleavage and early growth.

In this connection it is interesting to note that others have prepared an extract from sea-urchin eggs and larvae which is growth-promoting, (91) and one which is growth-inhibiting. As has also been found

with goldfish, the growth-accelerating principle seems to be associated with the protein fraction of the extract. When the whole extract is used, it is said to be growth-inhibiting and to produce the same results as overcrowding. The point I have made is that with the sea-urchin eggs, under the conditions of our experiments, there is also an ill effect of undercrowding, and that there is an optimum population size for speedy development which is neither too crowded nor too scattered.

Much similar work has been done with the effects of numbers on the rate of multiplication with various protozoans. Again I shall have to select results from the mass of available evidence. The late T. Brailsford Robertson (107) of Australia announced back in 1921 that when two protozoans of a certain species were placed together, the rate of division was considerably more than double that which resulted with only one present. It should be noted that during the time of these experiments and in all these protozoa which we are considering reproduction was entirely asexual, by self-division of the original animal. I subjected the data in Robertson's original paper to statistical analysis and found that there were only thirteen chances in a thousand of getting as great a difference by random sampling. Such results must be taken seriously (Figure 10).

They were. And the period after 1921 was enlivened for some of us by denials from one first-class laboratory after another that there was anything significant in Robertson's data. Robertson himself

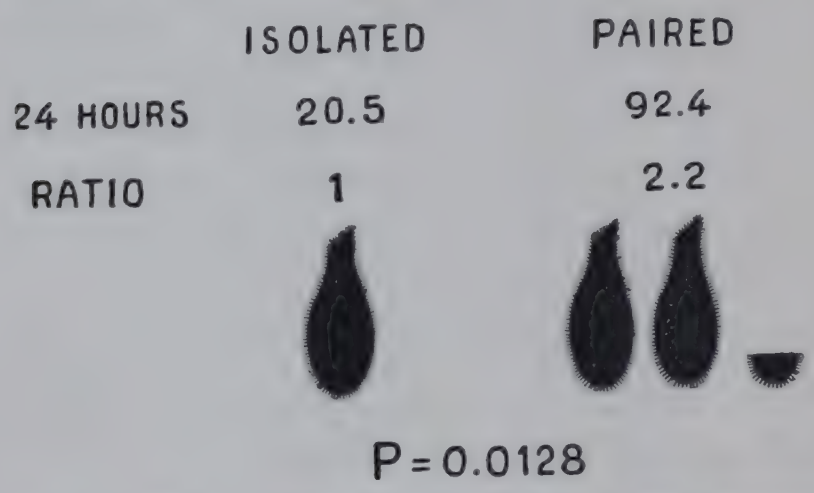


FIG. 10. Robertson found that when two protozoans were placed together each yielded over twice as many as when the same number of similar protozoans were isolated.

rechecked and confirmed his results, though his explanations of them tended to vary. For the moment we are not concerned with the explanations; but what are the facts? The first extensive corroboration from outside Robertson's own laboratory came from the work of Dr. Petersen at Chicago. When she cultured the common *Paramecium* in small volumes of liquid, she obtained the same results as had Robertson's critics, but when she used relatively larger volumes of the same culture medium, a cubic cen-

timeter more or less, she got an increase in division rate with the presence of a second individual, as Robertson had found it in the Australian form he had studied.

Still the critics were not convinced. Accordingly Dr. Johnson, now of Stanford University, repeated this whole study using a different protozoan, one of the *Oxytricha*. (68) When sister cells from pure-line cultures were used there was no difference at the end of the first day, whether the *Oxytricha* were introduced singly or in pairs into one or two drops of good medium. Later, the cultures started with one organism always were ahead. With larger volumes, two organisms showed a higher rate of reproduction per original animal at the end of the first day than if started with a single protozoan.

Again for larger volumes Robertson's results were confirmed, and those of his critics for smaller volumes. But Johnson had only started. He knew from the work of others that if a protozoan is washed through several baths of sterile water the associated bacteria are rinsed off. Then if the washed protozoan is put into a weak solution of the proper salts, into which has been introduced known numbers of the bacteria on which they normally feed, the problem can be studied with a controlled food supply, both as to kind and amount.

This he proceeded to do. He found a common bacterium on which his sterile *Oxytricha* would grow

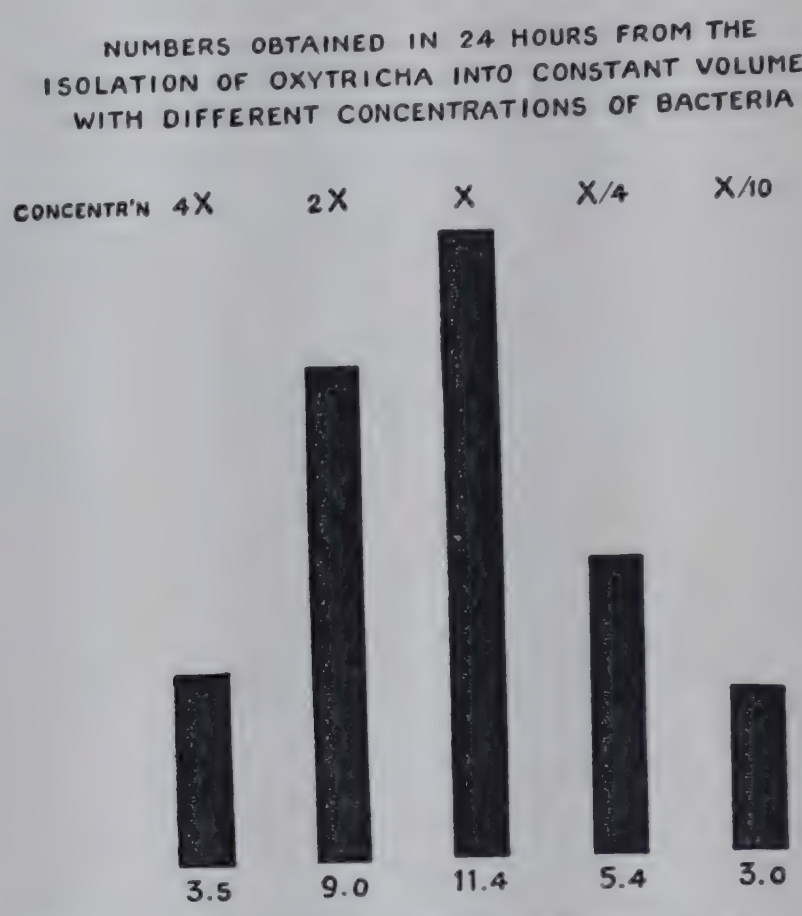


FIG. 11. The ciliate protozoan *Oxytricha* reproduces more rapidly with a certain limited number of bacteria present than with either more or fewer. (From Johnson.)

and reproduce faster than in the ordinary medium. He made standard suspensions of these bacteria in sterile salt solution, at what we may call an X concentration. The bacteria could reproduce little, if at all, in the salt medium, so that he knew how much

and what kind of fodder he was feeding his washed protozoans.

The results of varying the amount of food are

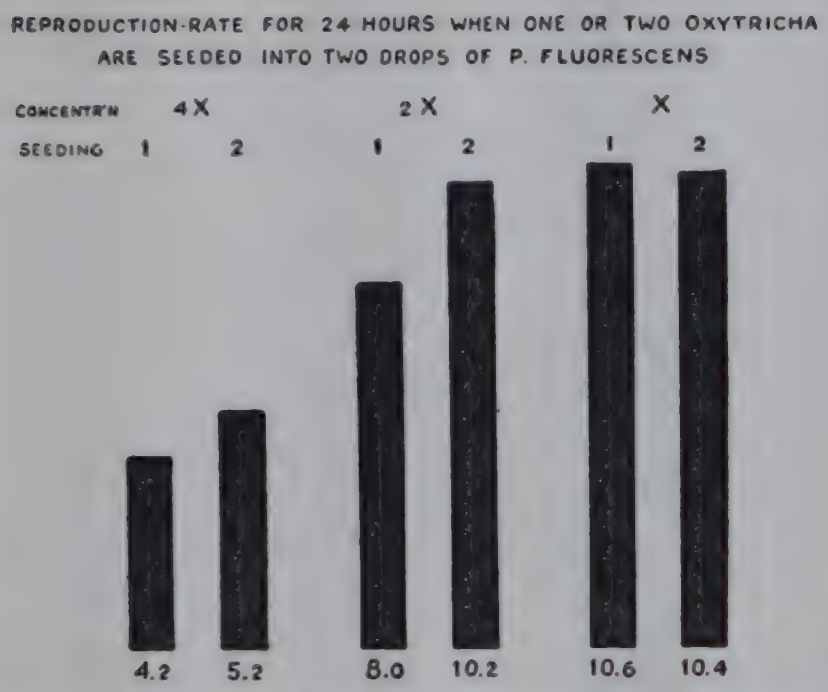


FIG. 12. In the denser suspensions of bacteria the protozoans divide more rapidly when cultures are inoculated with two protozoans than if started with a single individual. (From Johnson.)

shown in Figure 11. With X concentration, in twenty-four hours one animal produced about eleven progeny. With 2X concentration, isolated sister cells produced nine, and with a 4X concentration other isolated sister cells produced but three and a half. The rate of reproduction also decreased when less than X bacteria were present.

Now he was ready for the grand Robertson test, except that by this time nearly all the factors were controlled. The results are shown in the following figure (Figure 12). With X concentration it made no difference whether he started his small cultures with one or with two sterile animals. With 2X concentration, the cultures started with two individuals did as well as in X concentration, but those which were started with only one individual lagged definitely, producing only 80 per cent as many animals in twenty-four hours. With 4X concentration even the culture started with two *Oxytricha* was slowed down, but not so much as that started with only one. He had shown that in the presence of an excess number of bacteria, cultures seeded with more than one bacterium-eating protozoan thrive better than if but one is introduced. Not content with this Johnson took another species and tried it all over again with the same results.

From all this careful work we judge that the facts on this particular aspect of the effects of numbers present on the rate of asexual reproduction seem now to be straight; but what about their explanation? This, as it turns out, also interests us. Robertson advanced the following hypothesis to explain the results which he had observed. During division each nucleus retains as much as pos-

sible of an essential, growth-producing substance with which it was provided, and adds to it during the course of growth between divisions. At each division, however, this substance is necessarily shared with the surrounding medium in a proportion that is determined by its relative solubility in the culture water, and by its affinity for chemical substances within the nucleus. The mutual speeding of division by neighboring cells is due to each cell's losing less of this necessary substance because of the presence of the other. The more of this growth-promoting substance there was in the cell, Robertson thought, the faster would be the division rate; so that any circumstance which would conserve the limited supply would tend to speed up processes leading to cell division.

Stripped to essentials this hypothesis says that as a result of the presence of a second organism both lose less of an unknown something which is essential for division than would happen if but one were present. Returning to the problem after the criticisms of half a dozen years, Robertson affirmed that all the data and conclusions on the subject that had been issued from his laboratory remained valid save that they might apply to the associated food organisms and not to the protozoans themselves.

Johnson has paid considerable attention to this

problem, and has concluded that the results which he has observed can be explained as due to bacterial crowding; that the larger number of protozoans introduced into dense cultures thrive best because they are able to reduce the bacteria to density optimal to the protozoa faster than their isolated sister cells can; and therefore they show a higher rate of reproduction.

This does not seem to be the whole story; for from points as distant as Baltimore (79) and Jerusalem, (101) I have reports from trustworthy men that with still simpler protozoans they are getting results which suggest that some modification of Robertson's hypothesis may be correct after all. These organisms stimulate each other to more rapid growth merely by their presence in the same small space.

With fine courtesy, Professor Mast of Johns Hopkins has placed a report of his experiments in my hands in advance of publication and has permitted me to summarize his results. He finds that populations of a flagellate protozoan grow more rapidly in a sterile medium of relatively simple salts when larger numbers are introduced than if the cultures are started with only a few organisms.

I must not put too much stress on these reports, pending the appearance of yet more data, but I should expect to find here, as elsewhere, that com-

plicated problems such as these that deal with the rate of population growth are controlled by more than one mechanism.

The suggestions from the simpler protozoans, taken together with other aspects of the mass physiology of protozoa which have been only partially reviewed here, and with the acceleration of development demonstrated for sea-urchin eggs, encourage me to renew a suggestion made some years ago, (3) which has, so far as I am aware, been overlooked to date.

Let us go back to consider the case of external fertilization among aquatic animals. When spermatozoa and eggs are shed into sea water by sea-urchins or other marine animals, their length of life is distinctly limited. If a sperm fails to contact an egg during the fertilizable period, death results probably from starvation for the spermatozoa, perhaps from suffocation for the egg. This means that the animals of the two sexes must be fairly close together if there is to be a union of the shed sexual products. The most vigorous sperm of the sea-urchin *Arbacia* can travel in still water about thirty centimeters, that is, about one foot and two inches. (55) Spermatozoa of these animals diluted a few thousands of times can survive from three to twelve hours; the majority succumb by seven hours.

If a current catches it, such sperm can travel many times thirty centimeters, but even in sea water the sexes must be relatively aggregated if fertilization is to be successful. In fresh water, the life of shed gametes is much shorter. After ten minutes, eggs of the pike lose the power to be fertilized, (102) and the longevity of sperm of certain fresh-water fishes is said to be less than a minute, so that in fresh water the aggregation is even more essential. With animals that require internal impregnation the necessity for close co-operation between at least two individuals is obvious. Such considerations must be fundamental for the long-recognized breeding aggregations of animals, especially of those that shed eggs and sperm into surrounding water.

Mass relationships may be even more important sexually, and here I come to the new suggestion: perhaps they had a hand in shaping sex itself. Presumably sexual evolution started, as it does today in plants, with a time when all gametes of any one species were similar. Under these conditions a first step toward the union of two reproductive elements could be supplied by the greater well-being fostered by the presence of more than one gamete within a limited area, as even the simpler protozoans are stimulated to asexual division today by the near-by presence of another of the same species. In

the survival value existing for separate living cells before actual sexual union took place we can find a logical beginning for the action of selection, which would in turn, with present known values, result in the establishment of the sexual phenomena as they appear today. These fields have not been sufficiently explored to allow for more than this flash of imagination, which future researches may verify or discard.

At this point it would be well to pause and look back over the road we have traveled thus far. The charts, (7) shown as Figures 13A and B, show that most of our evidence has come from fairly well down among the simpler forms of life. I have called attention to mass protection of one sort or another among bacteria, planarian worms, goldfish and the simpler crustaceans. Actually there are in scientific literature good cases of mass protection for almost all the animals shown in these charts; and where exact information is lacking, as for example among the rotifers, this is a result only of lack of interest in conducting experiments on this point with these animals. I have little doubt that we could, overnight, demonstrate mass protection from colloidal silver for rotifers; but we have more interesting work to do.

I have also shown active acceleration of fundamental biological processes as a result of numbers present for sea-urchin eggs and larvae, and for various pro-

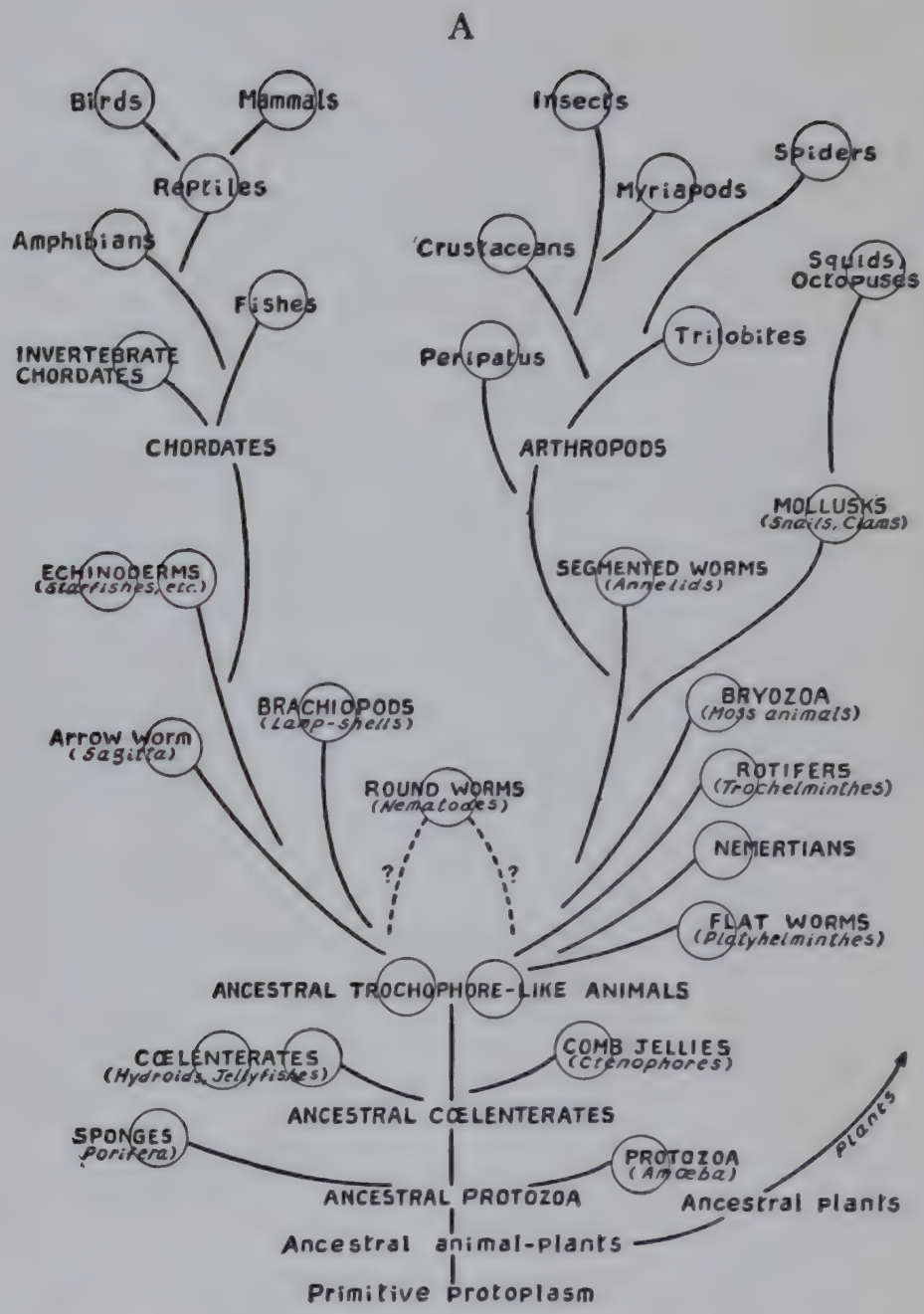
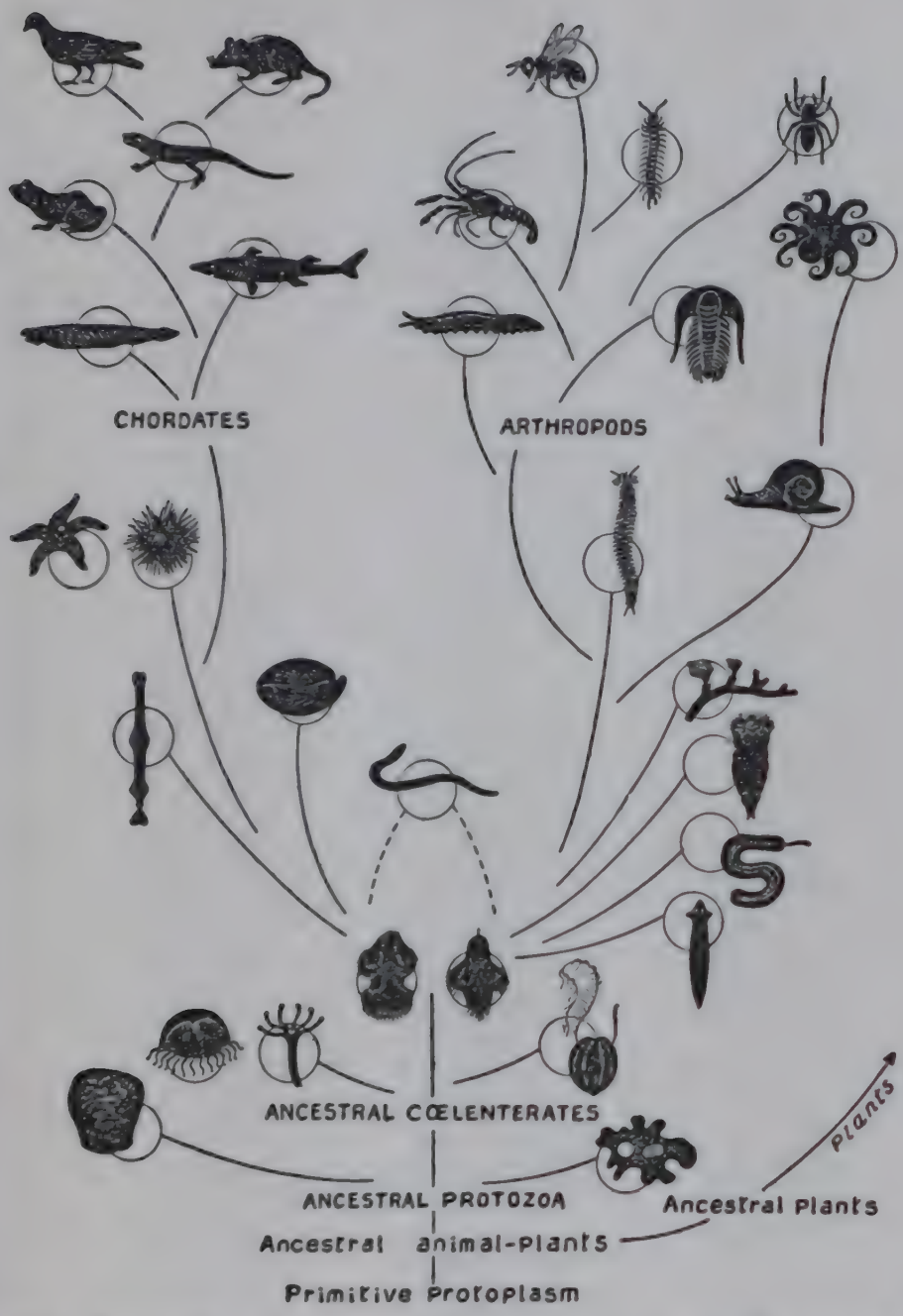


FIG. 13. A recent suggestion concerning the ancestral relations within the animal kingdom. The circles in A

B



and B allow cross-identification. (From Allee in *The World and Man.*)

tozoans. These have been given in some detail, which has not left time for similar demonstrations among regenerating cells of sponges; nor have I time to tell how hydra have been saved from depression periods by the use of self-conditioned water. I have mentioned but not elaborated the fact that grouped animals frequently have different rates of respiration as compared with their isolated fellows. This has been recorded widely in the animal kingdom, notably among planarians, certain lower crustaceans, some starfish, fishes and lizards, and for some, at least, associated survival values have been demonstrated. To this extent, then, I have given the crucial evidence I promised earlier that a sort of unconscious cooperation or automatic mutualism extends far down among the simpler plants and animals.

These charts should illustrate one other point. The insects stand at the apex of one long line of evolution; mammals and birds are at the peak of another line of evolution; the two have been distinct for a very long time. This view of evolution indicates that the ancestral tree of animals is not like that of a pine tree with man at the very top and insects and all the other animals arranged as side shoots from one main stem. Rather, there are at least two main branches which start low, as in a well-pruned peach tree. Both rise to approximately equal heights, indicating cor-

rectly that in their way the insects are as specialized as the birds or mammals. Since both insects and mammals have developed closely-knit social groups, this is further evidence that there is a widely distributed potentiality of social life. We shall return to this subject later.

IV. Aggregations of Higher Animals

A GREAT deal of skepticism is necessary in science, if progress is to be even relatively steady and sound. Not only must the scientist be skeptical of advance reports of new results until he has seen the supporting evidence, no matter how stimulating the thesis and how well it would explain material already gathered; but in fields which lie near his own researches it is necessary if possible to bring the problem into his own laboratory and there examine the validity of the evidence itself. This repeating of experiments in order to check the first observer is sometimes also a testing of scientific courtesy, but every real scientist must be prepared to submit to it with the best grace possible.

It is demanded also that from time to time one should be skeptical of views long held, and of the evidence on which they were built up, particularly of the inclusiveness of the conclusions that have been drawn. Without my own fair share of this skepticism I should never have been drawn into what I knew

from the beginning would be a long and laborious series of experiments concerning the effects of numbers present upon growth.

As long ago as the eighteen-fifties Jabez Hogg, (62) an Englishman, found by experimenting that crowding decreased the rate of growth of snails and produced stunted adults. From that day to this there has been almost no break in the reported evidence that overcrowding reduces growth; the number of reports that crowding in any degree increases growth are relatively few.

This phenomenon has, however, been observed by enough workers using animals widely distributed through the animal kingdom to show that the retarding effect of undercrowding on growth is real. Before considering the implications of this statement let me review briefly some of the evidence. (3) Here as elsewhere I shall make no attempt to catalogue all the available evidence; the list would be impressively long but tedious.

It is relatively easy to show that mixed populations of many animals grow faster than if the same number of some one species are cultured together. The common experience of aquarium enthusiasts that the presence of the snails in aquaria increases the rate of growth and well-being of their fishes is a case in point. Their rule-of-thumb experience has been fully

verified by careful laboratory experiments. A more crucial test involves individuals of the same species: all snails, let us say, or all goldfish. Is there some optimum size of the population at which individuals grow most rapidly?

For years I have been studying different aspects of this problem with the aid of a succession of competent, critical research assistants and associates. The names of these young scientists are interesting and, I think, important. They include Drs. Bowen, Welty, Shaw, Oesting and Evans, and Messrs. Livengood, Hoskins, and Finkel, all of whom have independently obtained the basic results I am about to describe. (13, 14, 76)

We have used goldfish for our experimental animals, because these are inexpensive, easy to obtain, hardy under laboratory conditions, and able to stand daily handling.

In order to have a consistently constant water we make up a synthetic pond water by dissolving in good distilled water salts of high chemical purity. Into such water goldfish about three inches long are placed in sufficient number so that they will give a conditioning coefficient of about twenty-five. Let me explain: this coefficient is obtained by multiplying the number of fish by their average length in millimeters and dividing by the number of liters of water

in the containing vessel. Living in this water the fish condition it by giving off organic matter and carbon dioxide. They are left in the water for twenty-one hours or so, while a similar amount of the same water stands near by under exactly similar conditions except for the absence of fish.

At the end of this time the clean control water is siphoned into a number of clean jars, and a small measured goldfish is placed in each. At the same time the conditioned water is siphoned, either with or without removing particles (that is, of excrement, etc.) that may be present, into similarly clean jars. A set of small measured goldfish, like those used in the control jars, are transferred into the conditioned water. These small "assay" fish have been feeding for about two hours before being transferred; the larger conditioning fish are allowed to feed for a somewhat longer time before being washed carefully to remove food residues and replaced in another lot of water to condition that.

Meantime the jars, 120 of them, are all washed carefully; and after this is done the experimenter has nothing more to do until the next day, except to put the laboratory in order, keep the temperamental steam distilling apparatus running, test the water chemically in several ways, keep his records in order,

and otherwise see that nothing untoward happens to make him or anyone else question the results.

After some twenty, twenty-five or thirty days of such care, in which Sundays are included, again each fish is photographed to scale, as they were also photographed at the beginning of the experiment; the photographs are measured and the relative growth determined for the fish that have daily been placed into perfectly clean synthetic pond water, as compared with those which daily have been put into conditioned water, that is, into the water in which other goldfish have lived for a day.

During the course of an analysis of this problem we have performed this simple basic experiment many times. The first forty-two such tests involving 886 fish gave on the average about two units more growth for the fish in the conditioned, slightly contaminated water, than for those in clean water (Figure 14). These results have a statistical probability (P) of about one chance in a hundred million of being duplicated by random sampling. Hence we have demonstrated that under the conditions of our experiments the goldfish grow better in water in which other similar goldfish have lived than they do when they are daily transferred to perfectly clean water.

The problem that has been occupying us for some

time is why this is so. What are the factors involved that make this slightly contaminated water a better medium for young goldfish than a clean medium?

We have said that the conditioning fish are fed

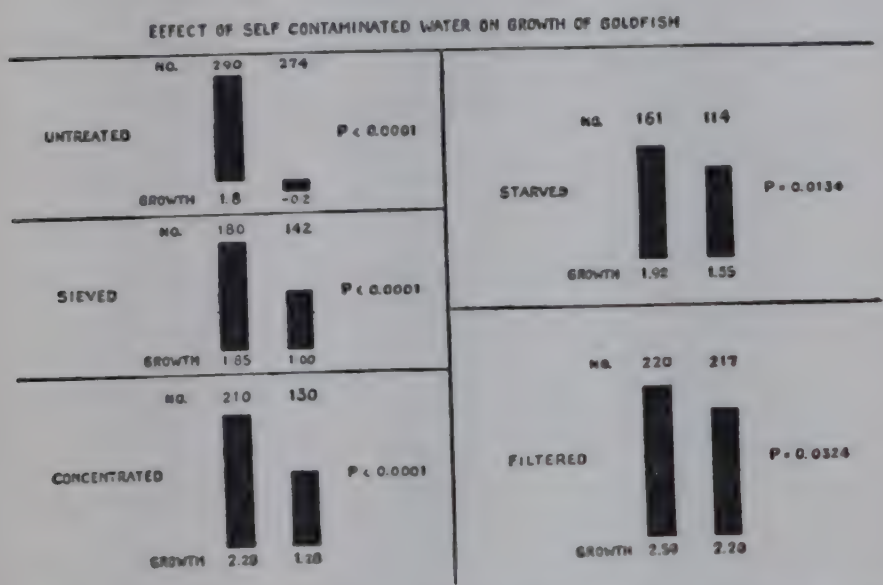


FIG. 14. Goldfish grow more rapidly if placed in various kinds of slightly contaminated (conditioned) water. The numbers above the columns show the number of fish tested. The longer column represents the growth in conditioned water.

for two or more hours daily and are then washed off and placed in a fresh batch of water. Although the fish are never fed in the water they are conditioning, within a few hours after their transfer into it from the feeding aquarium the water becomes more or less cloudy with regurgitated food particles. These bits of food are large enough so that the growth-assay

fishes can strain them out of the water. When such particles are removed by filtering, the growth-promoting power of the conditioned water is greatly lessened, but it is not completely lost. In our experiments we found that suspended food particles accounted for 80 per cent or more of the increased growth in conditioned water over that given in clean control water.

These experiments give certain suggestions concerning some other conditioning factors that may be acting. For example, we know that the skin glands of fish secrete slime (Figure 15). When we have made a chemical extract of this material we have frequently recovered a growth-promoting substance, apparently a protein, which was effective in stimulating growth when diluted 1 to 400,000, or even 1 to 800,000 times. At these dilutions it is not probable that this factor is affecting growth by furnishing food material.

There are, of course, other possibilities, many of which we have checked. The increase in growth is not due, for example, to a change in the total salt content of the water, for this does not change in our experiments; nor to differences in acidity or oxygen, nor, so far as careful quantitative analyses have revealed, to changes in chemical elements present. We may be dealing with some sort of mass protection, such as was discussed in the last chapter, in which

the conditioning fishes remove some harmful substance, but of this we have no real evidence.

Whatever the explanation, we are certain of the facts, and we know that we have demonstrated a de-

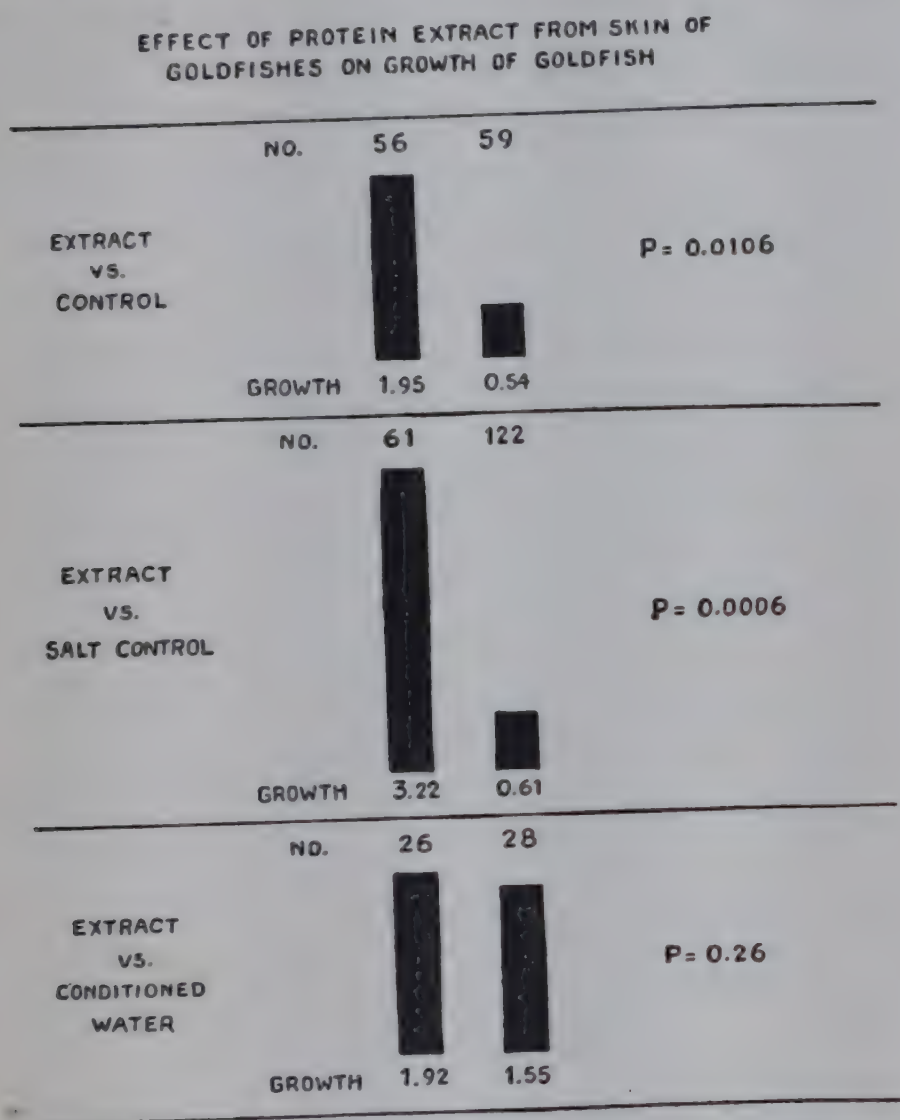


FIG. 15. An extract from the skin of goldfish frequently has growth-promoting power. The arrangement of the figure is on the same plan as was used in Fig. 14.

vice such that if in nature one or a few fish in a group find plenty of food, apparently without willing to do so they regurgitate some food particles which are taken by others, a sort of automatic sharing. Again, in water that changes rapidly, such stagnant-water fishes as goldfish, if present in numbers, are able to condition their environment, perhaps by the secretion of mucus, so that it becomes a more favorable place in which to live and grow.

Perhaps I have lingered too long over this one case; I am so close to the facts and to the tactics used in collecting them that they may seem more interesting to me than they will ten years hence. We have run the same experiment with positive results with a few other species of fishes; and we have also found by experimentation that certain fish will regenerate tails that have been cut off if several are present in the same water more rapidly than if each is isolated. (112) The same is true for the young tadpoles of salamanders, with which we have had experience. The explanation of the more rapid regeneration of such cut tails is probably relatively simple. The several animals together more readily bring the surrounding fresh water to approximately the salt content of the cut and regenerating tissues than can be done by a single animal placed in the same amount of water.

This may not be the whole of the story but it is probably a significant part of it.

In both of these cases the additional growth of aquatic animals, which occurs as a result of the presence of other animals of the same species, is produced in response to some sort of chemical which has been given off into the surrounding water. This may be nothing more than the unswallowing of surplus food by the conditioning fish. With animals whose tails have been freshly cut off the addition of salts to the water by the group may balance the osmotic tension at the cut surfaces and so favor re-growth. The exciting result of these studies lies in the suggestion that some less obvious growth-promoting substances may also be secreted into the surrounding water.

Animal aggregations frequently produce physical as well as chemical changes, and while we are considering the effect of numbers of animals present on the rate of growth of individuals it is interesting to examine one case in which growth-promotion appears to have been produced largely by changes in temperature. Such an effect has been reported more than once; it is most simply illustrated in a warm-blooded animal, this time the white mouse. The experiment was first performed in Poland, but the causal factors were then only partially recognized. It has been re-

peated in our laboratory where significant steps have been taken towards its further analysis.

Vetulani, the original experimenter, (117) used closely inbred mice for his experimental animals. He measured the growth of males and females separately from the sixth and on through the twenty-second weeks of their lives. After rearrangement he followed them for ten weeks longer as a sort of control. Fresh food was supplied in abundance each day, and proper experimental conditions seem to have been maintained.

Growth during the first sixteen weeks of the experiment is shown in the accompanying graphs (Figure 16). All started off at approximately the same rate. After the fifth week of the experiment, however, it is clear that the isolated mice were growing most slowly, and they continued to do so as long as the experiment ran. The most rapid rate of growth was observed in those mice which were placed two to four per cage; those five to six per cage grew next best, and only slightly below these came those living nine to twelve per cage.

Under the conditions of this experiment the isolated young mice were most handicapped, those most crowded were next, while those that were somewhat but not too crowded grew most rapidly. When the mice were rearranged for a continuing period of ten

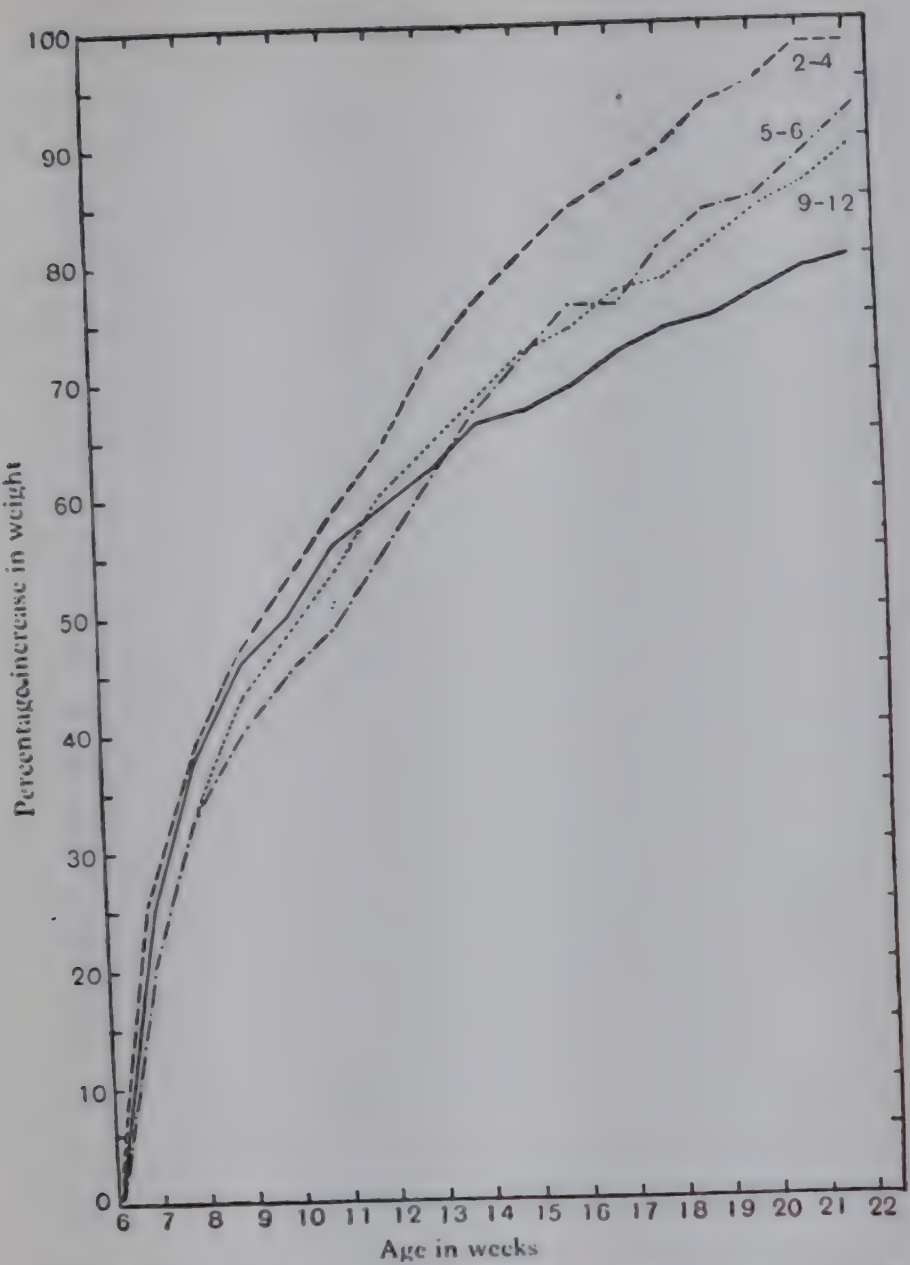


FIG. 16. White mice grow faster in small groups than in large ones; they grow slowest when isolated (solid line). (From Vetulani.)

weeks the same relations held, showing that it was the state of aggregation rather than individual differences between mouse and mouse which was important in producing the differences in growth rates.

Mr. Retzlaff, (105) the student who brought this work into our laboratory, tried first to repeat Vetulani's experiments in a room held at relatively high temperatures (29-30° C.). Under these conditions he found that insofar as significant differences existed they showed that most rapid growth occurred with the isolated mice. When, however, he lowered the room temperature to about 16° C. he obtained the same general effect as reported by Vetulani. It would seem then that in this case the opportunity to keep warm in a chilling temperature is one of the main factors in promoting growth of the crowded, but not too crowded, animals. This conclusion is strengthened by recent analyses of the temperature relations of mice, made by French physiologists, (30) which show that a mammal as small as a mouse has great difficulty in maintaining a constant temperature and rarely does so for extended periods of time. A change of external temperature from 30° to 18° C. will cause a lowering of 0.4° in the body temperature of a resting mouse.

With such temperature lability it is easy to see that a few mice huddled together as is their habit could

help each other maintain their internal temperatures, conserving energy for growth, while if isolated they must use much of their energy in keeping warm.

Vetulani observed another factor at work. Some of his mice had lesions of the skin which they treated by licking. When these were in the head region they could only be treated by another individual. Some of his isolated mice had such lesions when at the end of the first experimental period they were re-grouped for further observation; these wounds were soon cured by their new nest mates.

When one turns from studying the rate of growth of individuals to that of populations of these higher sexual animals, many of the same principles can be observed working as were outlined in the last chapter for the growth of asexual populations of protozoans in which overcrowding retards population growth, while optimal crowding, at least in many instances, favors it.

With experimental populations of mice, for example, three long, laborious experiments made in Scotland (36) and in Chicago (106) have indicated that, under the conditions tried, the least crowded mice reproduce most rapidly. The same holds true for the well-studied fruit-fly, *Drosophila.* (96)

Neither with these flies nor with the mice is there any indication to date of a more rapid rate of repro-

duction per female when more than the minimal pair is present. I have a strong suspicion, however, that one would get a more rapid rate of increase per number of animals involved if, instead of keeping the sexes equal in numbers, there were a ratio, let us say, of two females to one male.

We do know that with *Drosophila* the greatest numbers are produced when the feeding surface is relatively great but not too great; (60) this result may be explained by the assumption that with too great space, or in other words, with too few flies present, wild yeasts or molds grow more rapidly than the *Drosophila* can keep under control.

Another well-studied laboratory animal, the flour beetle, *Tribolium,* under certain experimental conditions gives most rapid population growth at an intermediate population size rather than with too few or too many present. A study of data collected by Chapman showed that in a flour beetle's little world, a microcosm of thirty-two grams of flour, these beetles, during the early stages of population growth, reproduce most rapidly per female with two pairs present (Figure 17). Reproduction is more rapid when four pairs or even sixteen pairs are present, than if there is only one pair. (3)

This work of Dr. Chapman's was done for another purpose. We took it for an indication of possibilities,

and Dr. Thomas Park looked into the matter independently. (88) He found the situation very much as it had originally appeared to be. A Scotsman named Maclagen had a curiosity along the same line

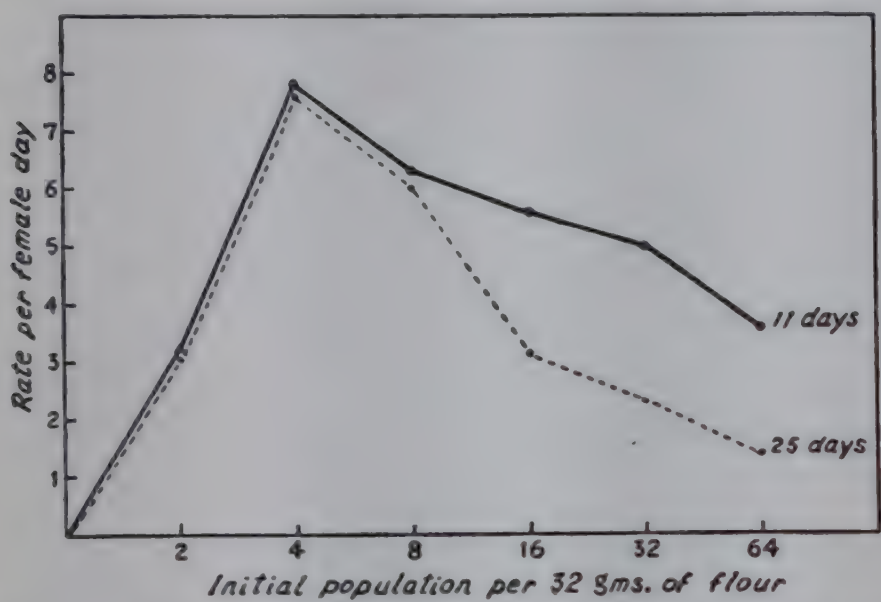


FIG. 17. Flour beetles reproduce more rapidly if more than one pair is present.

and independently re-checked the whole matter with the same results. (77) Three separate workers in three different laboratories have now obtained essentially similar results with these same beetles, and the chances that all are mistaken are rather remote.

One of them, Dr. Thomas Park, has proceeded to analyze the factors involved. (89) He finds that the results come from the interaction of two opposing tendencies. In the first place, adult beetles roam at

random through their floury universe. They eat the flour, but they may also eat their own eggs as they encounter these on their travels. This habit of egg-eating tends to reduce the rate of population growth, the more so the denser the population.

The second factor is the experimentally proven fact that up to a certain point copulation and successive re-copulation stimulate the female *Tribolium* beetles to lay more eggs, and eggs with a higher percentage of fertility. Thus the more dense the beetle population the more rapid its rate of increase. The interaction of these two opposing tendencies results in an intermediate optimal population in which more offspring are produced per adult animal than in either more or less dense populations.

It may be felt that I have been keeping too closely to the more or less artificial conditions found in the laboratory. It is true that in an attempt to bring the various aspects of the population problem under experimental control we have avoided those field observations which can only be recorded as more or less interesting anecdotes. We have now come to a point in our inquiry, however, at which it is necessary to move directly into the field.

Given the evidence at hand, that optimal numbers present in a given situation have certain positive survival values and some definitely stimulating effects

on the growth of individuals and the increase of populations, we strike the problem of the optimal size of a population in nature. This is an exceedingly difficult question on which to obtain data. Suppose, therefore, that we simplify it by asking what minimal numbers are necessary if a species is to maintain itself in nature?

This inquiry is a direct attempt to find under natural conditions the application of the statement by Professor Pearl that "this whole matter of influence of density of population in all senses, upon biological phenomena, deserves a great deal more attention than it has had. The indications all are that it is the most important and significant element in the biological, as distinguished from the physical, environment of organisms."

Over and over again in the last half-dozen years I have asked field naturalists, students of birds, wildlife managers, anyone and everyone who might have had experience in that direction, how few members of a given species could maintain themselves in a given situation. Always until this last summer I have found that, stripped of extra verbiage behind which they might hide their ignorance, the real answer was that they did not know.

And then I had two pieces of luck; I found a man and a scientific paper. My friend, Professor Phillips

of South Africa, came to spend some weeks with us. He told us that the Knysna Forest, a protected woodland in South Africa, has an area of 225 square miles, fifteen miles on a side, and that this forest is the home of a herd of eleven elephants, which can also range outside the forest limits. On the other hand, the Addo Forest, of twenty-five to thirty square miles, supports a herd of twenty-four elephants. (98) Dr. Phillips thinks that the smaller herd is not maintaining itself, and that the larger one, under apparently less favorable conditions as regards available area of range, is at approximately the lower limit for keeping up its own numbers. He estimates that an elephant herd of about twenty-five individuals could maintain itself in an unrestricted range providing civilized man were absent.

He gave us a second example, of a herd of some three hundred springbok on a protected reserve of six thousand acres in the Transvaal, which was unable to maintain its numbers and became reduced to eighty or ninety, on its way toward total extinction.

It is well known that in the life of equatorial Africa the tsetse fly plays an important part. It carries the trypanosomes which cause the deadly disease, "sleeping sickness," of man and his domestic animals, and which affect native game as well. The British

colonial governments have been active in attempts to control the density of these fly populations. In general they are restricted to damp, low-lying forest. In districts where this is confined to the borders of water-courses, and hence where the fly belt has naturally a definite limit and is restricted in size, an ingenious fly trap has been used successfully. The trap takes advantage of the natural reactions of the tsetse fly. These are strongly positive to a slightly moving dark object a few feet above ground. With appropriate screening they can be caught as they fly toward such an object; they will fly up and fall back until they literally wear themselves out. It was at first thought that such a trap would be helpful chiefly in reducing the excess fly population; then, to the delight of the control officials, they found that when in these restricted fly belts the tsetse flies had been trapped down to a certain minimum population there was no need to catch the very last flies; below the minimum level those remaining disappeared spontaneously from the area. Nor did they return unless brought back in considerable numbers accompanying movements of game, or as a result of the slow extension of range from other infested areas. The work of the control officials in such regions thus was very much easier than had been anticipated.

Two pertinent cases concerning the minimum

number below which a species cannot go with safety have come in part under my own observation. In 1913, my first summer at the Marine Biological Laboratory at Woods Hole, Massachusetts, the veteran scientists of the laboratory, at least those who still were willing to exhibit naturalistic enthusiasms, were greatly pleased at the visit of a flock of laughing gulls to the Eel Pond near the laboratory. The main breeding ground of these gulls is on Muskeget Island off Nantucket. In 1850 the laughing gulls were abundant there; but they were exposed to the depredations of egg takers and later, about 1876, to the attacks of men interested in obtaining their striking wings and other feathers to satisfy the millinery demand for feathers of native birds, which was then at its height. (49) Under this slaughter the colony was nearly wiped out; at its low point about 1880 there were not more than twelve pairs of laughing gulls left on Muskeget Island, and only a few of these bred. A warden was employed in a somewhat extralegal capacity by certain ornithologists who regretted seeing the species die out, and he was assisted by the captain of the local life-saving crew in protecting the gulls from raids. Later changes in laws regarding protection of birds and the use of plumage in millinery gave more secure protection for the growing colony. For the first ten years the birds increased

slowly, but thereafter more rapidly, until there are now thousands breeding on the island, and their range has spread to the mainland. In Woods Hole, at the present time, these birds whose return in 1913 excited so much comment are as common as the terns. In this case, a few breeding pairs, nesting in a relatively safe place, were able to regenerate the local population in less than fifty years; all that was needed was protection from the predations of man.

The nesting colonies of gulls have attracted attention from many; a report by Darling has recently appeared concerning certain relations between numbers of herring gulls in a colony and breeding behavior, and survival of young gulls on Priest Island off the northwest coast of Scotland. (39) There are indications that the members of larger colonies stimulate each other to begin mating activities earlier than when the colonies are smaller and, what is apparently more important, there tends to be a shorter spread in the time from the laying of the first egg until the last one is laid. This means that the breeding activities are more intense while they last.

The period between hatching and the growth of the first adult plumage is a crucial time in the life of young gulls. While they are in the downy stage they are preyed upon by outside predators; also at

this time the gull chicks that wander from their home nests may be pecked to death by other members of the colony. The toll of the chicks is comparatively less, the shorter the time from the hatching of the

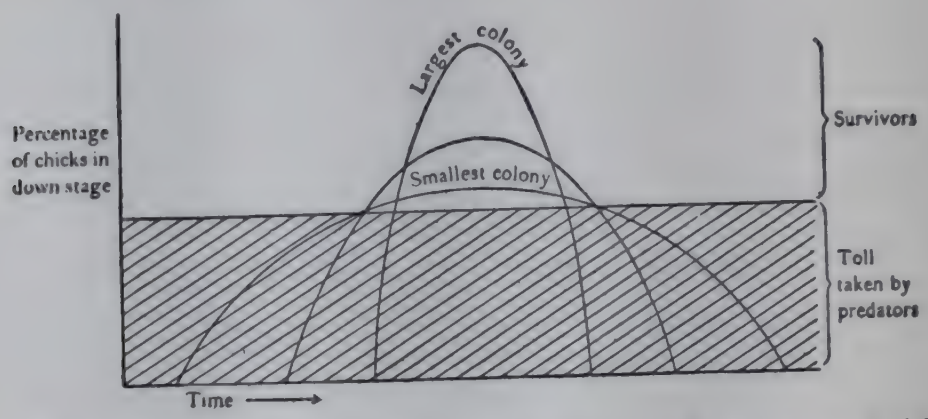


FIG. 18. The "spread" of time in which eggs are laid in a colony of herring gulls affects the percentage that survive. The smaller the colony the longer the spread, and the fewer survivors. [From Darling (39) by permission of The Macmillan Co.]

first fuzzy young gull until the last one changes to a young fledgling with adult feathers. These relations are graphically shown in Figure 18.

Darling thinks that the greater success of the larger colonies does not lie in any vague factor of mutual protection, but in the nearer approach to simultaneous breeding throughout the colony. This is a phase of social facilitation which will be discussed more fully in a later chapter.

These observations need to be extended and con-

firmed. They suggest one mechanism, that of mutual stimulation to mating, which may have operated to produce social nesting among birds, and which seems capable of giving added survival value to the larger colonies, once the habit of collecting into breeding flocks is established. We have here a suggestion that these social colonies of birds have evolved far enough so that there has come to be a threshold of numbers below which successful mating does not take place. The numbers that constitute this threshold probably vary under a variety of conditions.

In one case, when only two pairs were present, nests were built but no eggs were laid, while in a more favorable season, with three pairs, eggs were laid and one chick out of eight that hatched lived through the downy stage.

I saw the laughing gulls myself at Woods Hole last summer; and I also found a paper by Gross giving the case of another almost extinct population which could not be revived. The heath hen, probably a representative of an eastern race of the prairie chicken, was formerly very abundant in Massachusetts, and may have been distributed from Maine to Delaware, or perhaps even further south. It was gradually isolated by the killing of birds in the intermediate region and was driven back, until about 1850 it was found only on Martha's Vineyard and the near-by

islands, and among the pine barrens of New Jersey. (56) By 1880, except for attempted and unsuccessful introductions elsewhere, it was probably restricted to Martha's Vineyard. In 1890-92 it was estimated that one hundred to two hundred birds remained on that island. Then several things happened at about the same time: prairie chickens were introduced and probably interbred with the vanishing heath hen, protection of the birds was stiffened, and collectors' prices went up! It is an interesting commentary that most of the museum specimens, of which 208 are known at present, were collected between 1891 and 1900, when the probable extinction of the heath hen was noised abroad. This is one of the modern handicaps of small numbers; let a species or race become known to be rare, and museum collectors feel it their special duty to get a good supply laid in, just in case it does become extinct.

By 1907, when the Heath Hen Association was formed and employed a competent warden, the count had been reduced to seventy-seven. Massachusetts became aroused and purchased six hundred acres of heath hen range and leased a thousand acres more. The reservation was near a state forest which added another thousand acres of protected range. The birds responded to increased care and by 1916 it was estimated that there were two thousand in existence.

Then came a fire, a gale, and a hard winter, with an unprecedented flight of goshawks, and in April, 1917, there were fewer than fifty breeding pairs. The next year, when there was an estimated total population of 150, the heath hen range was invaded by several expert photographers who took motion pictures of mating behavior. In the face of this disturbance at a critical time, still a good year allowed the birds to increase and again to spread over Martha's Vineyard. In 1920, 314 were counted; but thereafter a decline in numbers set in which was never stopped. The figures for those five successive years are: 117, 100, 28, 54, 25. At this point extra wardens were put on the job, who killed more cats, crows, rats, hawks, and owls, the enemies of the heath hen. The next year's count was 35; in 1927, there were 20; but in 1928, in a census that lasted four days, only a single male was found. No other bird was seen thereafter, though a reward of a hundred dollars was offered for the discovery of another. This single male was banded and released and was last seen alive on February 9, 1932. With his death the heath hen became extinct. (18)

When this much is known of the decline in numbers of a given species there should be some knowledge of the factors involved in its extinction. There is. In the earlier years, as I have indicated with re-

gard to museum collecting, there was undoubtedly a considerable amount of poaching; but as population of heath hens declined, local sentiment turned in favor of protection and poaching decreased, both because of a more intelligent public reaction to the birds, and because of closer patrol by wardens. Dr. Gross, whose account I have been following, thinks that there was evidence of an inadaptability of the species, an excessive inbreeding, and, at the end, an excessive number of males. In such small populations the sex ratios frequently become highly abnormal. Disease and parasites took their toll. Predators, particularly cats and rats, were active. The females hid their nests well and were faithful in remaining on them, so that they were killed off by the fires which at times whipped over the breeding grounds.

Over sixty thousand dollars was spent in trying to save the heath hen, but without success. In contrast to the laughing gull, which nested in a relatively safe place and which came back from a population as low as the heath hen's until the very last, this unfortunate species was not able to adjust itself and continue existence, even with as intelligent human help as could be mustered in its favor.

The general conclusion seems to be that different species have different minimum populations below

which the species cannot go with safety, and that in some instances this is considerably above the theoretical minimum of one pair.

By way of the laboratory, the coastal regions of Massachusetts, and South African grassland and forest, we are arriving at a general biological principle regarding the importance of numbers present on the growth, survival and, as we shall see, upon the evolution of species of animals.

Lacking definitive information on this last phase of the subject, we shall turn to mathematical explorations of its possibilities, as made primarily by Professor Sewall Wright. (127, 41) Although the ideas to be presented are essentially simple in principle, they are sufficiently novel and unfamiliar to challenge the closest attention.

I shall not indulge here in the details of the mathematical analyses, for the very good reason that I do not understand them. If I were not convinced, however, that Professor Wright does understand them I should not present this outline. It is only fair to say that, in my opinion, in dealing with these ideal populations Professor Wright cannot bring into sharp focus at one time all the factors that may be acting in nature. This is what he has been courageous enough to attempt; the more nearly he succeeds, the more likely is the calculation to be too complex for

presentation in detail except to highly specialized readers.

The environment is in a state of constant flux and its progressive changes, whether slow or fast, make the well-adapted types of the past generations into misfits under present conditions. The result may be rectified either by the extinction of the species, if it is not sufficiently plastic, or through reorganization of the hereditary types. In such a reorganization the simple Lamarckian reactions apparently do not operate; that is to say, when confronted with new, critical conditions, species cannot go to work and produce needed changes to order. The reactions are much more complicated than that.

To present the modern interpretation of this reorganization I need three technical terms which I shall define before using. *Genes* are bits of protoplasm too small to be seen through the microscope, which are located in all cells and which are thought to be the bearers of heredity. They behave as indivisible units, that is to say, a gene if present in an organism is either transmitted as a whole or not at all. *Gene frequency* is the term applied to the frequency with which a given gene is found in a population, relative to the total possible frequency (two in every individual). By *mutation* is meant a large or small hereditary change which appears suddenly,

usually in the sense in which I shall use it, as a result of a change in one or more genes. With these three terms in mind we are ready to try to understand how the hereditary types may become reorganized.

Such a reorganization implies a change in gene frequencies. By this I mean now that there will be a decrease in the abundance of the genes which were responsible for the past adaptations that are now obsolete, and an increase in the frequency of those genes which allow an adaptation to the new conditions. Gene frequencies remain constant in a large population unless changed by mutation, selection or immigration. This is because of the unitary character, without blending, and the symmetry of the Mendelian mechanism of heredity.

These life-saving genes may have been present in the species for a million years as a result of long past mutations, without having been of any value to the species in all that time. Now under changed conditions they may save it from extinction. It is important to note that organisms do not usually meet changed conditions by waiting for a new mutation; frequently all members of a species would be dead long before the right change would occur. This means that since a species cannot produce adaptive changes when and where needed, in order to persist

successfully it must possess at all times a store of concealed potential variability.

I may interject parenthetically that at times this appears to call for the presence of a considerable number of individuals as a necessary condition to provide the needed variations. A part of this reserve of variability may be of no use under any circumstances; some characters may be useful, some may never meet with the circumstances under which they would have survival value; while others, though of no use or even harmful when they appear, may later enable the species to live under newly changed conditions.

Hereditary changes tend to be eliminated as soon as they run counter to decided environmental selection. In large populations the results of mutations tend to stabilize about some average gene frequency, which represents the interaction between the rate of mutation and the degree of selection. Frequently mutation pressure pushes in one direction and selection in another and the resulting gene frequency in the population represents a point or zone of equilibrium between these forces. In small populations which are not too small, selection between genes becomes relatively ineffective, and the gene frequencies drift at random over a wide range about a certain mean position. In very small breeding popu-

lations, even though these may be small isolated colonies of a large widespread species, gene frequencies drift into fixation of one alternative or another more rapidly than they are changed by selec-

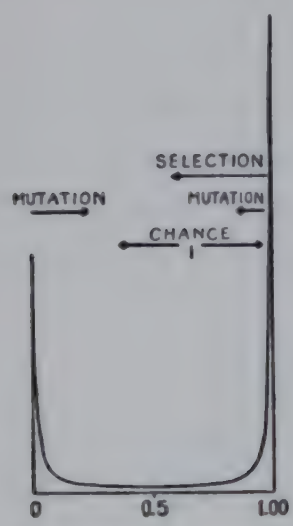


FIG. 19. In small populations, genes drift into fixation or loss largely irrespective of selection; the frequency of fixation or loss depends in the long run on the relative frequency of mutation and reverse mutation. (After Wright.)

tion or by mutation. Mutation, however, prevents permanent fixation. The condition at any given moment is largely a matter of chance.

Perhaps a diagram will help at this point. In Figure 19 the horizontal axis shows the different gene frequencies in a population, and the vertical axis gives the chances of the population under consideration possessing any given gene frequency. At the left,

the gene frequency is zero; that is, the gene in question is absent from the population for the time being. The height of the curve shows that there is a good chance of this happening. At the extreme right the gene has become fixed and all animals in the population have it; they are a pure culture so far as this gene is concerned. Again there is a high degree of probability that this may happen when numbers are few. But the intermediate condition, when the gene is present in some but not all of the animals, shows little chance of occurrence.

In such small populations, as has been said before, the gene frequency is determined mainly by chance; any given hereditary unit tends to disappear completely or become fixed and occur in all members of the small inbreeding colony. Such a condition may have been reached in the inbred population of the heath hen on Martha's Vineyard.

With populations that are intermediate in size there is a greater variety of possibilities. Some genes are lost, others reach chance fixations, and others fluctuate widely in frequency from time to time. These conditions are shown in Figure 20.

If a given species is isolated into breeding colonies in such a way that but little emigration occurs between them, a condition known to exist in nature, in the course of time, as Professor Wright shows, the

species will become divided into local races. This will happen although at the time of separation the populations were all homogeneous and the environment of all remains essentially similar.

If the environment does remain steady the larger

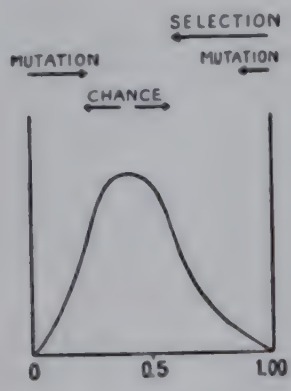


FIG. 20. In medium populations, gene frequencies drift at random about an intermediate point but not so much so that complete fixation or loss is likely to occur. (After Wright.)

colonies will tend to keep the same hereditary constitution as that which the whole species formerly had. (Figure 21.) Small breeding colonies will, however, become pure cultures for different characters, and it is impossible to predict the course of the hereditary drift in any of these populations. As illustrated in Figure 20, the fixation will be a matter of chance, and local races will result without any necessary reference to adaptation.

The snails in the different mountain valleys of Hawaii afford the classical illustration of this point.

Each individual mountain valley has its separate species of snails. They are distinguished by size, by color markings, and by other characters which may be wholly non-adaptive.

Colonies which are intermediate in size will pre-

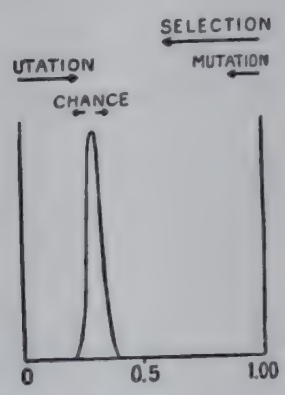


FIG. 21. In large populations, gene frequency is held to a certain equilibrium value as a result of the opposing pressures of mutation and selection. (After Wright.)

serve a part of the variability that will be lost in the smaller colonies. Even so, there will be some independent drifting apart of the various gene frequencies, so that these, too, will give rise to new local races. Professor Wright's calculations show that with mutation rates of the order of 1:10,000 or 1:100,000, such intermediate populations, optimal for evolution, will consist of some thousands or tens of thousands of individuals.

With small breeding populations, then, genes tend to become fixed or lost. Even rather severe selection

is without effect. Individual genes drift from one state of fixation to another regardless of selection. In large populations, gene frequencies tend to come to equilibrium between mutation and selection, and if selection is severe, there tends to be a fixation of the gene or genes that carry adaptive modifications, and evolution comes to a standstill.

With a population intermediate in size, when there are enough animals present to prevent fixation of the genes on the one hand, but on the other, not enough animals to prevent a random drifting about the mean values determined by selection and mutation, then evolution may occur relatively rapidly. The results obtained will depend upon the balance between mutation rate, selection rate, and the size of the effective breeding population.

In one more case the effect of differences in severity of selection was worked out by Professor Wright (Figure 22). With a moderate mutation rate, if the selection is relatively weak, mutation pressure may determine the result and the given character will then drift to fixation or, as shown in the diagram, to extinction. As selection pressures increase, selection tends to take charge of the end products, and, if slight, there is a wide variation about a mean; if more intense, the amount of variation becomes less and less.

When a species is broken up into different breeding colonies, as it is with the snails in the Hawaiian

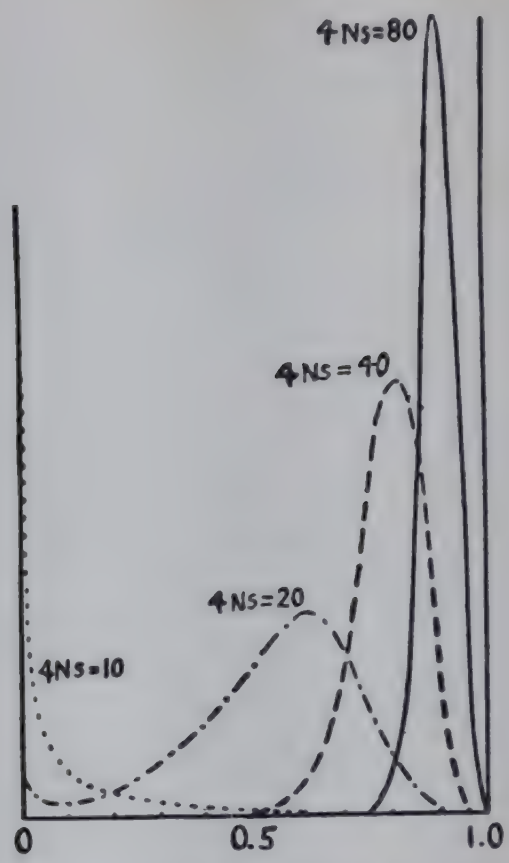


FIG. 22. As intensity of selection increases it becomes more and more dominant in determining the end result, and the degree of variation is lessened; 4Ns gives selection pressure. (From Wright.)

valleys, (57) it can be similarly shown that the effects produced depend on the rate of emigration between colonies, as well as selection pressure, mutation pressure, and population size, other factors being constant. Cross-breeding introduces genes into a popula-

tion in a way that is essentially identical with mutation in its mathematical consequences; however, similar results may be obtained in a much shorter time by cross-breeding. And in fact all the different results which have just been illustrated can be duplicated by varying the numbers of the emigrants.

This is not the place to explore all the implications and possibilities of these interesting analyses. The highly significant conclusion has been reached that if a species occurs not as a single breeding unit but broken into effective breeding colonies which are almost isolated from each other, the members of different colonies, given sufficient vigor, may evolve into dissimilar local races. If one of these becomes well adapted to its environment it may increase in numbers and send out numerous emigrants. If these emigrants find and interbreed with members of other less advanced colonies they will grade these up until they resemble the most adapted colony. This part of the process resembles a stock breeder's grading up of a mediocre herd of cattle by repeated infusions of new and improved "blood" into his herd. The significant thing here is that the random differentiation of local populations furnishes material for the action of selection on types as wholes, rather than on the mere average adaptive effects of individual genes.

The end results will vary even when the original

population was homogeneous, and when mutation rates are similar throughout, even though selection is in the same direction in all parts of the different colonies. The primary factor under these conditions will be that of effective breeding population size, and there will be greater chance for varied evolution among the populations that are intermediate in size, as contrasted with those which are small or large, and still greater chance for evolution when a large species is broken into small breeding colonies which are not completely isolated from each other.

This argument, even as I have simplified it, is not too easily followed the first time one goes over it. Perhaps my use of an old teaching trick, that of repetition of the same ideas with different words and different illustrations, may be forgiven. In doing so I am still leaning heavily on Professor Wright. The series of diagrams shown in Plate IV are built on one fundamental background. In perspective we see two elevations, one higher than the other, and two depressions which are the low points in a valley between the two peaks. Every position is intended to represent a different combination of gene frequencies. The peaks represent gene combinations which are highly adaptive; the depressions represent those that lack adaptive value. The degree of adaptiveness is shown by the height occupied by the given

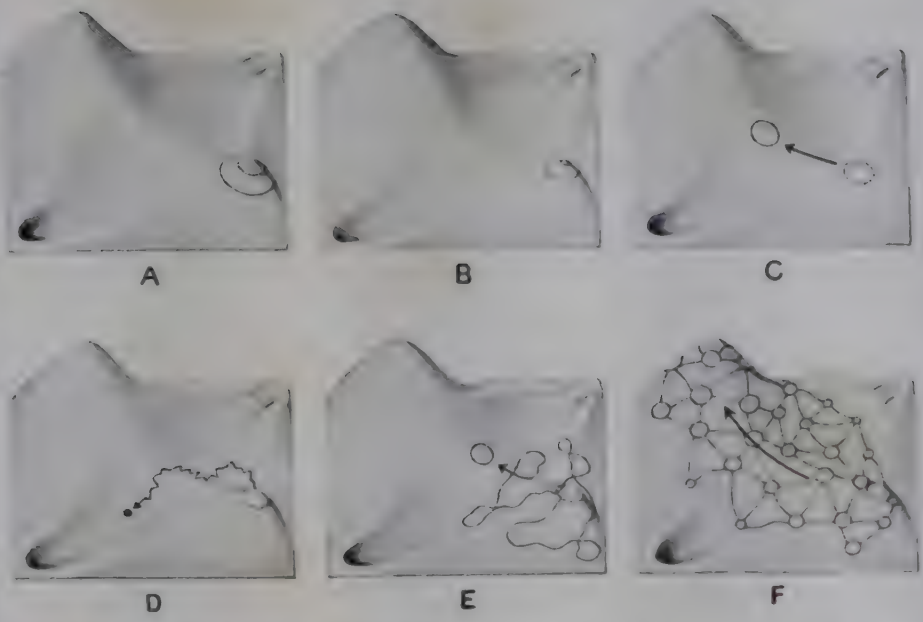


PLATE IV. A population originally possessed a set of gene combinations of some slight adaptive value (dotted line). With increased mutation rate it can expand to less adapted levels (A); with increased selection it contracts (B); if the environment changes the gene frequency must shift (C); with small numbers and close inbreeding the course of evolution is erratic and extinction usually follows (D); with larger numbers, evolution takes place more readily (E); most readily, when a large population is broken into local colonies with inter-emigration (F). (Modified from Wright.)

population. The variability of the population is shown by the size of the area that is occupied. Every individual in a species may have a different gene combination from every other, and yet the species may occupy a small region relative to all the possibilities.

We may call the lower peak Mount Minor Adaptation and the higher one Mount Major Adaptation. In Figure A we find a population which is fairly well-adapted, but not so much so as if it occupied the higher peak. Its original position and its variability are shown by the dotted circle. As a result of increased rate of mutation or of reduced selection, or both, the variability of the population has increased and it now spreads down to lower positions on this Mount Minor Adaptation. It contains more aberrant individuals and even freaks than when subject to less frequent mutation or to more severe selection, and a freak may appear that is more adaptive; but this important end has been achieved at the expense of the variability which might have made a major advance possible.

Figure C introduces a different situation. As a result of environmental change Mount Minor Adaptation has disappeared and the adapted population has been able to move to a new location at about the same level formerly occupied; now it is on the slope

of Mount Major Adaptation, and if selection continues may be expected to move up that adaptive peak. A continually changing environment is undoubtedly an important factor in evolution.

The effects of population size are illustrated in the next three diagrams. The general background is the same as in Figures A and B. In Figure D is shown the effect of a decided reduction in population size, and consequently in variability, in the species that formerly occupied Mount Minor Adaptation. It is in fact so small that selection has become ineffective and the different hereditary qualities shift to chance fixations. As non-adaptive characters become fixed at random the species moves down from its peak over an erratic, unpredictable path. With reduction of population size below a certain minimum, control by selection between genes disappears to such an extent that the end can only be extinction.

With the species population intermediate in size, with the same mutation and selection rates as before, gene frequencies move about at random but without reaching the degree of fixation found in the preceding case. Since it will be easier to escape from low adaptive peaks, the population will tend finally to occupy the more adapted levels. The rate of progress is, however, extremely slow.

Finally, in Figure F, we see the case of a large

species which has become broken up into many small local races, perhaps as a result of restricted environmental niches. Each of these local races breeds largely within its own colony, but there is an occasional emigration from one to another. Each tends, if it is small in number, to give rise to different variations which shift about in a non-adaptive manner. The total number of relatively stable variations will be much greater since the total number of individuals is so much larger than in E. Under these conditions the chances are good that some of the local colonies will escape from the influence of Mount Minor Adaptation and manage to cross the valley to Mount Major Adaptation. Here the race will expand in numbers and will send out more and more emigrants which will interbreed with the stocks in the less adapted colonies and tend to grade them all up toward a higher adaptive level.

The conclusion is as Professor Wright says: "A subdivision of a large species into numerous small, partially isolated races gives the most effective setting for the operation of the trial and error mechanism in the field of evolution that results from gene combinations."

In the rate of evolution, therefore, population size is as important as we have seen it to be in the growth

of individuals or in the growth of population numbers; and the optimal population size does not coincide with either the largest or smallest possible but lies at some intermediate point.

V. Group Behavior

IN THE second chapter I told of how I stumbled on the fact that in the breeding season the normal behavior of isopods is affected by numbers present. Such effects have long been known for many types of behavior, and it would not be profitable here to catalogue and analyze all the cases that are on record. Rather, as before, I shall select certain well-authenticated examples of breeding reactions and of other types of behavior. Those which are chosen are especially noteworthy because of the behavior pattern which is involved, or because freshly observed, or both.

And here is a shift in emphasis. I have been stressing the existence of a widespread, fundamental automatic co-operation which has survival value, and have given evidence that it is a common trait in the animal kingdom. In this chapter I shall discuss group behavior which may or may not have immediate survival value. In each instance, and throughout the discussion as a whole, I shall be engaged in trying

to find to what extent behavior is influenced by the presence of others, and shall not consistently attempt to assay possible values which may or may not be involved.

With many more or less social animals the group up to a certain size facilitates various types of behavior. This is frequently called social facilitation.

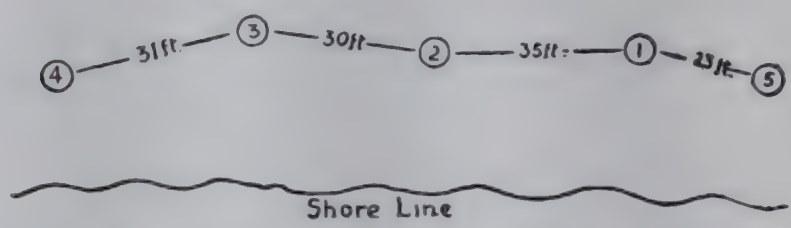


FIG. 23. Manakin males establish rows of mating courts in the Panamanian rain-forest. (From Chapman.)

One phase of social facilitation is illustrated by some observations of the mature student of birds, Frank E. Chapman, (28) near the tropical laboratory on Barro Colorado Island in the rain-forest of Panama. Mr. Chapman found that males of Gould's manakin establish lines of courting places (Figure 23). The manakin is a small warbler-like bird, delicately colored and relatively inconspicuous. Each of the courting places is occupied by a single male; the line thus formed extends for many yards through the undergrowth of the rain-forest. From time to time each day during the long nesting season, the males resort to their individual cleared spots on the forest

floor and make their presence known by a series of snaps, whirrs and calls which may be heard as far as three hundred yards. The females, who are more quiet and retiring, apparently are attracted by the line of males; they come individually from the surrounding thickets and each mates with one of the males. The evidence suggests that they are attracted from a greater distance by the spaced aggregation of males than they would be by isolated courting places. The more or less organized line of males in breeding condition apparently facilitates the mating of these jungle birds.

This is a highly specialized example of the widespread phenomenon of territoriality which can be recognized even among breeding fishes, (103) and which has been much studied of recent years in birds. (65) Typically the male birds arrive first in the spring and take up fairly well-defined territories in the same general area, which they defend from intruding males. Then the females come in and flit from territory to territory before settling down to raise a brood with one particular male. There is always the strong suggestion that the presence of a number of singing males, even if spaced about in different territories, attracts and hastens the acceptance of some one of them by an unmated female.

Group stimulation of the amount of food taken

has been reported for various animals, including rats, (59) chickens (23) and fishes. (118) I shall illustrate by some of the experiments conducted in our laboratory by Dr. J. C. Welty. These have been

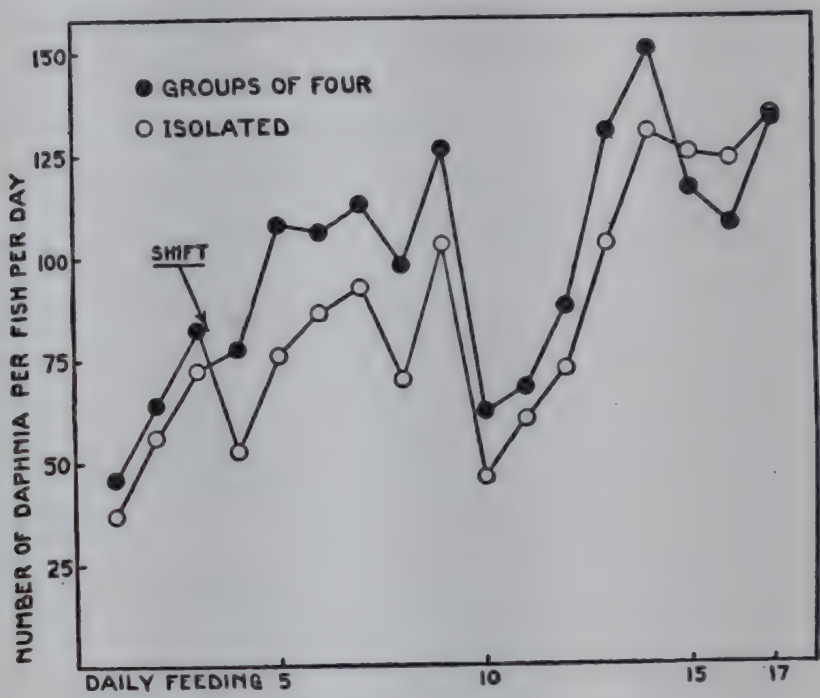


FIG. 24. Many kinds of fishes eat more if several are present than if they are isolated. (From Welty.)

amply verified by other research workers. In connection with experiments on the effect of numbers on the rate of learning in fishes, which will be discussed later, Dr. Welty undertook to find whether grouped fish ate more or less than if they were isolated. The results of a typical experiment are illustrated in Figure 24.

Goldfish were photographed to scale, and those of

similar size were selected for experimentation. Two groups of four each were placed in separate crystallizing dishes and eight others were isolated each into a wholly similar dish. The different dishes were separated by black paper so that vision from one to the other was impossible. A known number of the small crustacean, *Daphnia,* were introduced daily into each dish. These living *Daphnia* had been screened so as to select the large animals only. As shown by the figure, fish in all groups of four ate decidedly more on the first three days of the experiment. At this time the two lots were shifted. Those that had been grouped were now isolated, and vice versa. There was an immediate shift in the numbers of *Daphnia* taken, with the newly isolated animals now eating less than the accompanying groups. This indicates that we are dealing with an effect of numbers present rather than with chance differences in individual appetites. This difference kept up steadily until the last three days of observation, when an interesting complication arose. By this time the grouped fish were receiving a total of over six hundred *Daphnia* daily, including those which were eaten and the extras added to insure an economy of plenty. Each isolated fish was receiving only one-fourth as many. Now six hundred and more large *Daphnia,* each about an eighth of an inch long, make quite a swarm

in a none-too-large crystallizing dish. The consumption of food per animal by the grouped fish fell off, and as was shown by appropriate tests, this was due to the action of a so-called confusion effect. When fewer *Daphnia* were present, a fish might be observed to swim after an isolated crustacean and eat it, whereas a dozen *Daphnia* or so in the immediate field of vision seemed to offer conflicting stimuli that blocked the feeding response. Working on this suggestion, one group of four was given the usual quota of some six hundred *Daphnia* all at once; another group was given only one hundred at a time, and when these were approximately all eaten then another hundred would be introduced, and so on until the end of the regular feeding period. This prevented the *Daphnia* from being too dense at the beginning of the hour's feeding time. The isolated fish were fed as usual. Under these conditions the grouped goldfish which were fed one hundred *Daphnia* at a time ate definitely more than those given the whole confusing mass at once.

Here we come upon two, not one, mass effects. In the first place we see that the fish in groups of four were stimulated to eat more food than if isolated, and this depended on their state of aggregation. But, incidental to this demonstration, we find that in the presence of too many animated food particles a con-

fusion effect arises which decreases the feeding efficiency of the fish.

It has been suspected for years that such a confusion effect exists and has survival value for small animals flocking together in the presence of a predator, such as small birds in the region of a hawk. These observations of Welty's make the best demonstration that I know of the existence of such an effect, in this case the *Daphnia* in the presence of the fish. I am less interested in this confusion effect at present than in the demonstration of social facilitation in feeding, a phenomenon which has been shown to exist for a number of fishes, including zebra fish, paradise fish, goldfish and guppies of the more usual aquarium varieties, and the lake shiner, *Notropis atherinoides,* as well.

None of these fishes is very social, that is, none of them group into close schools. For evidence of similar social stimulation among social animals it is interesting to examine the effect of numbers present on the digging behavior of the highly social ants. The account of this work was published in 1937 by Professor Chen of Peiping, China. (29)

These ants, a species of *Campanotus,* dig their nests in the ground. It was found that all the worker ants of this species are capable of digging a nest when in isolation, but that the rate of work varies

with different individuals. If marked ants, whose reaction time has been tested in isolation, are placed together in pairs or in groups, they will start work sooner and will work with greater uniformity than if alone.

With oriental patience, Professor Chen and his assistants collected and counted the number of the tiny pellets of earth which were dug by different individual ants when isolated, and when members of groups of two or three ants. They found that the number of pellets removed is greater when the ants work in association with others than when each works alone. This accelerating effect is greater for slow than for rapid workers; when ants with intermediate working tendencies were tested (Figure 25) they were found to be speeded up when in company with a rapid co-worker and relatively retarded when placed with a slowly working ant. Interestingly enough, there was no difference between the stimulating effect of one additional ant and of many ants on the rate of work of a given individual. The social facilitation seemed maximum for these digging tests when only a second individual was present.

Ants which regularly work rapidly were found to be physiologically different from those that work more slowly. The faster workers were more susceptible to starvation, to drying, and to exposure to ether

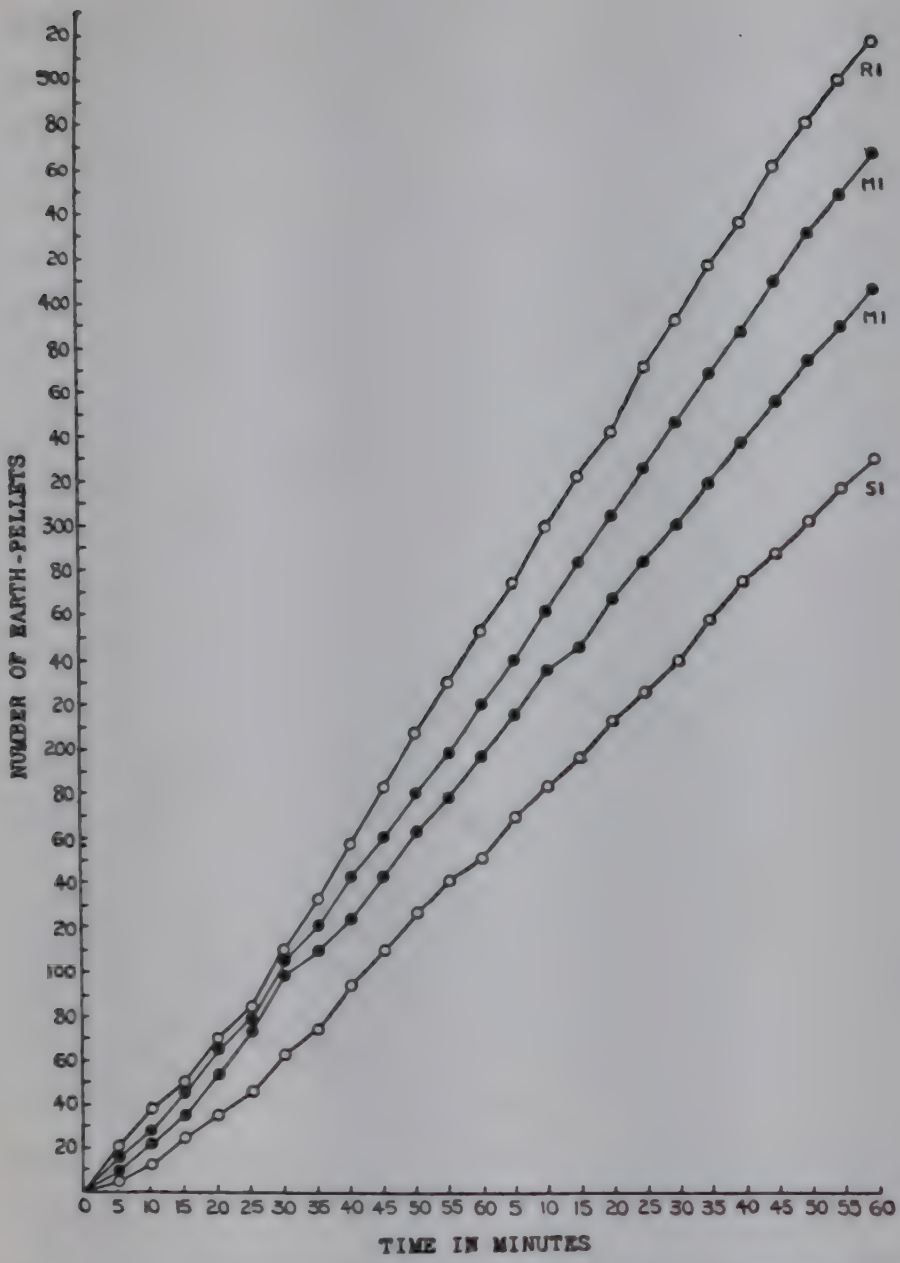


FIG. 25. An ant which works at an intermediate rate (M1) may be speeded up if placed with an ant which works more rapidly (R1) and slowed down if put with a slower worker (S1). (From Chen.)

or to chloroform. Tests that have been made by others indicate that animals that are more active physiologically usually succumb sooner under such adverse conditions, just as these rapidly-working ants were found to do. These are exceedingly interesting results because here we see that ants with apparently innate differences in speed of fundamental processes are affected in their speed of digging by the presence or the absence of a nest mate. The ant of intermediate speed, presumably with an intermediate underlying reaction system, is most interesting of all, because it can be either speeded up or retarded according as it is placed with an active or a more passive individual.

In this connection it has been known for over a decade scientifically what was common sense before that time, namely, that human animals, whether adults or children, can accomplish more mental and physical work, at least of certain kinds, and will work with greater uniformity when in association with others doing similar tasks, than if obliged to work in isolation. (15, 84)

Such considerations lead directly to problems concerning the effect of numbers present on the rate of learning in man. Here we find a set of questions that have great and immediate human significance. The world over, the training of the young animals of their own species is one of the major preoccupations

of mankind. This is particularly true in the United States, where we are engaged in mass education on an unprecedented scale. This teaching of the young to the extent to which we are attempting it is an expensive business in time, in effort and in money. We need to know, therefore, the number of these interesting young animals that can be trained together with best results. In other words, what is the optimal class size for the various levels of training from pre-school days through the preparation for the doctor's degree and further?

In part, the proper answer to this question calls for a statement of educational objectives. The development of strong individuality, for example, is not necessarily accomplished by the same teaching methods and class size which favor the growth of conformity to group patterns; and the rapid development of mastery of so-called skills may call for different number relations than those needed for the mastery of logical thought.

Even without positive information we can guess that the tutorial method with individuals or very small groups will best serve some ends while others will be achieved most readily in larger groups. The question, or a simplified part of it, thus becomes: What class size favors optimal rate of learning of the usual class material presented at different ages?

As might be anticipated, the difficulties of human experimentation being what they are, it is hard to collect accurate information on this point. Much depends on the comparative accuracy of the sampling, and also on more subjective factors, such as the attitude of the teacher and of the students toward large and small classes. There is also a factor which I have not seen mentioned in the literature on the subject, the effect on the student of realizing or suspecting that he is an object of experimental interest, an educational guinea pig. This stimulus is more likely to be potent, in my opinion, when the student is a member of a class which is unusual in size.

In the more careful studies, results of which have been published, the class numbers have ranged from "small" through "medium" to "large." The "small" experimental classes apparently have about twenty to twenty-five members; this represents a more usual experience to the student, and he is more likely to be conscious of class size when he is a member of a large class of seventy-five or more than when he is in a small class or a medium-sized one of thirty-five to forty. The sizes that are counted "large" or "small" vary greatly, sometimes in the same experimental treatment, so that frequently the comparisons are between larger and smaller classes, both medium in size, rather than between real extremes in numbers.

Frequently, too, the teaching practice varies in the two classes. Thus in one experiment the smaller classes in high-school geometry contained about twenty-five, while the large ones had about one hundred members. In the large classes a student helper was present for every ten class members. These helpers were superior students in geometry of the preceding year. As nearly as I can discover, there were no student helpers in the small classes. Under the conditions it is perhaps not unexpected that a better showing was made by those in the large classes. With them, there were present not only more instructors per student but these were people of nearly their own age, who could be approached without hesitation not only in class but out of class and even out of school hours. Every mature teacher knows that even with the best intention and the most democratic attitude, age differences widen the gap between the teacher and the taught, whatever other compensations there may be.

The most comprehensive experiments I have seen reported in this field are those of the sub-committee on class size of the committee on educational research at the University of Minnesota. (66) These were carried on at the college level and involved 109 classes under twenty-one instructors in eleven departments of four colleges in the University of Min-

nesota. Forty-two hundred and five students were observed in large classes, and 1,854 in small ones; of these 1,288 were paired as to intelligence, sex and scholarship before the experiment began. One of each pair was assigned to a large and one to a small class in the same subject taught by the same instructor. In this way the obvious variables were controlled as well as is humanly possible, unless we could have a large number of identical twins with which to experiment.

In 78 per cent of the experiments a more or less decided advantage accrued to the paired students in the large classes, and at every scholarship level tested, the paired students in the large sections did better work than their pairs in the smaller ones; the excellent students appeared to profit somewhat more from being in large classes than their less outstanding fellows.

Of the available data, a re-examination of the summaries indicates that there is on the average a difference in the means in the final grade of 4.1 points, favoring the students in the larger classes. There is a statistical probability of matching this by random sampling of four chances in ten million ($P = 0.0000004$), and this despite the fact that the majority of the class comparisons did not give significant differences when considered alone.

The numbers in the smaller classes usually ranged from twenty-one to thirty, but in some classes dropped as low as twelve; in the larger classes there were usually thirty-five to seventy-nine students; in the largest, one hundred and sixty-nine. Under the conditions which prevailed in these classes in psychology, educational psychology and physics, the students in the larger class sections made slightly but significantly higher final grades than those in smaller sections of the same subject taught by the same instructor.

So much for objective experiments. It happens that subjective estimates, made both by teachers and by students at Minnesota, favor the smaller rather than the larger classes. It was even true that the students were better satisfied with the marks received in smaller classes than they were with the slightly higher grades given them in the larger sections.

The general attitude seemed somewhat like that toward a friend of mine who teaches general mathematics at Purdue University. He is an experienced and excellent teacher. His program for one semester required that he should meet a normal-sized class of thirty to thirty-five at eight o'clock, and that at nine o'clock he should meet a class of double the size in a larger room, to repeat the same subject matter.

At the close of the semester the two sections were asked to rank the instructor on many different points. Uniformly the students in the larger section rated him lower than those in the smaller section, in such matters as teaching skill, pleasantness of voice, neatness of appearance and personal attractiveness!

I have had a fairly extensive teaching experience, which has included work in grade- and high-school teaching, as well as over twenty-five years of teaching at the college and university level, during which time I have taught classes of almost all sizes, from those of over six hundred at the University of California to the graduate classes of three or four that come my way; and I must confess to a personal prejudice against these very large classes. Even when using the same lecture notes, I do not give the same lecture to five hundred students that I give to forty or fifty. On the other hand, even with graduate classes and advanced seminars I am prejudiced in favor of having enough students, which means at least eight to ten, to give a certain *esprit de corps* to the group. Such personal opinions have their value, particularly when they click with experimental results such as those outlined by Hudelson from the experiments at Minnesota. It is unfortunate that those experiments did not test either the upper or the lower limits of class size which are conducive to good class-

room performance on the part of the students; and I know of none that does test these points adequately.

Some of the difficulties which are inherent in experimentation on the effects of class size on the rate of learning in man can be obviated by the use of non-human animals. This procedure does not solve all the requirements for elegant objective experimentation, and has the additional real difficulty of eliminating all possibility of adding subjective impressions to objective findings, a point which makes one of the strongest arguments for experimentation on man when feasible.

In some respects the most completely controlled experiments on the effect of numbers present on the rate of learning are those that Miss Gates and I performed some years ago, using common cockroaches as experimental animals. (52) Earlier work by two independent investigators had shown that cockroaches can be trained to run a simple maze, and can show improvement from day to day. In our experiments we found that the cockroaches could be trained to run the maze we used by fifteen to twenty-five successive trials on a given day, and showed definite improvement both in time taken to run the maze and in number of errors. However, unlike the experience of our predecessors, these University of

Chicago cockroaches could not carry over the effects of training from one day to the next.

The reason for this difference between our cockroaches and those around St. Louis and in Germany is not known. It may be that at the University of Chicago, despite our reputation for scholarship, the local cockroaches have a low IQ, or it may be that since we used animals from the bacteriological laboratory, because of their unusual size and physical vigor, we were unconsciously selecting the dumber sort. Or perhaps, contrary to our plan, we set them a problem which is intrinsically more difficult for the cockroach mentality. In any event, it is important to remember that our cockroaches forgot overnight anything they may have learned the day before. As it turns out, this was fortunate for the experiments we were carrying on, because we could match up individual cockroaches with the same speed of learning in pairs or groups of three for later tests without fear of a carryover from their previous experience.

The maze used is shown in Figure 26. It consisted of a metal platform from which three runways extended, each about two inches wide and a foot or so long. The two side runways ended blindly, but the center one led to a black bottle, which allowed the cockroaches to escape from the light. This apparently

was a reward for cockroaches which, when possible, give a negative reaction to light.

The three-pronged set of runways was mounted about half an inch above a pan of water, which the majority of the cockroaches tended to avoid, and so kept on the runways. The tests were all made in a

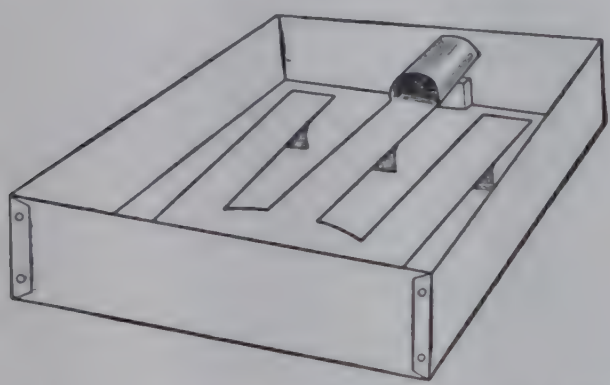


FIG. 26. A simple maze used in training cockroaches.

dark room and light was furnished by a single electric bulb mounted just above the point where the central runway left the main platform. In other words, the cockroaches, which are negative to light, had to learn to run through the area of strongest illumination in order to reach the dark bottle which served as a reward. After two minutes' rest in the dark bottle the cockroaches were literally poured out onto the platform of the maze without being touched by the experimenter, and observation of them began again.

The problem as set was about at the limit of cock-

roach ability. Approximately one-third of the insects tested never learned to stay on the maze; whenever they were placed on it they proceeded immediately to run off into the underlying water. Of the two-thirds

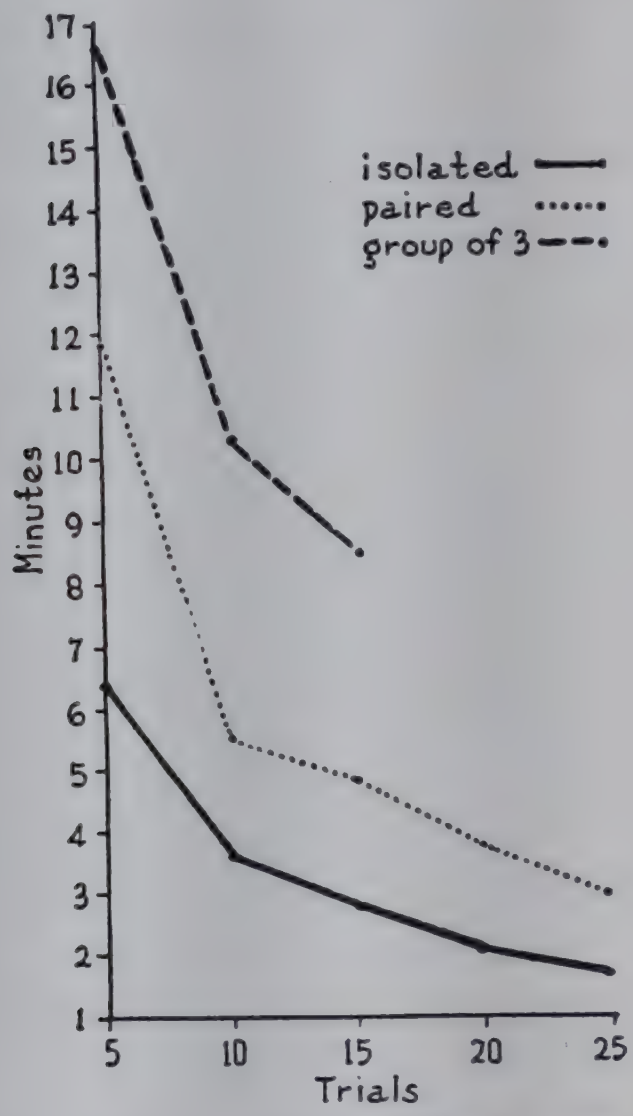


FIG. 27. Isolated cockroaches make fewer errors on the maze than the same animals paired, and still fewer than if three are being trained together.

that did learn to remain on the maze, a half, or another third of all those tested, did not show improvement in speed of reaching the bottle, after repeated

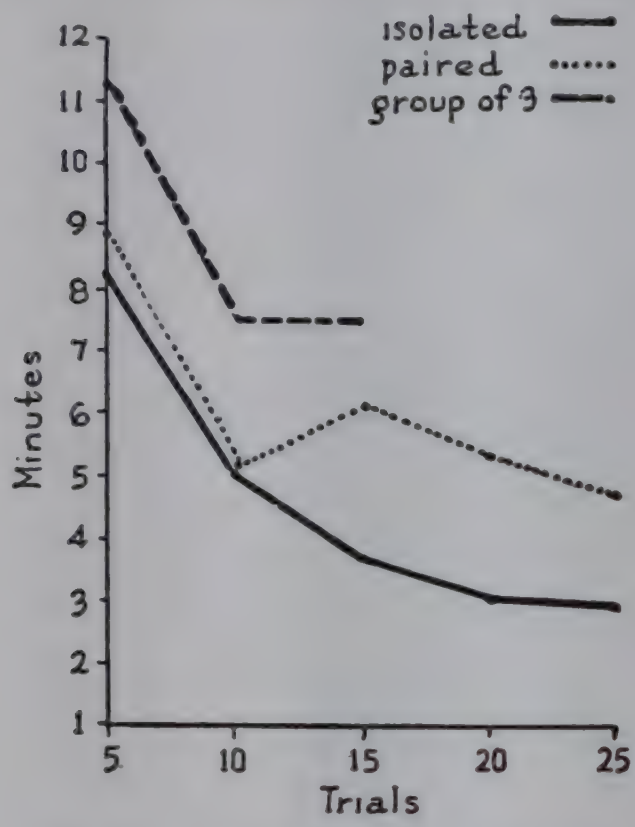


FIG. 28. They also take less time.

trials. Thus only one-third of the cockroaches we tested showed improvement with experience, and, as I said before, they forgot overnight all that they learned during the day.

As shown in the summarizing graphs (Figures 27 and 28), isolated cockroaches made fewer errors per trial throughout the whole training period. They

also took less time to run the maze than when the same animals were members of pairs or of groups of three. Turning the comparison around, paired cockroaches took longer time per trial and made more errors than when isolated, and groups of three took still longer and made more errors than those in pairs.

A study of the rate of improvement shows that during the early part of the training, as is indicated by the slant of the graphs, so far as time spent is concerned, paired cockroaches improved more rapidly than they did if isolated or in groups of three, and those placed three together on the maze improved somewhat more rapidly than they did when isolated. Thus, while the presence of one or two extra cockroaches slowed down the speed of reaction on the maze and increased the number of errors made at all times, yet the rate of improvement in speed of reaction was higher when more than one was present. There was, however, no significant difference in rate of improvement as measured by number of errors.

Excluding this one aspect of rate of improvement in time spent on the maze, in all other phases of the experiment isolated cockroaches turned in a better learning performance than they showed when more were present. Evidently under the conditions of our experiments the tutorial system usually works best with cockroaches.

Essentially the same sort of experiment was tried with isolated and paired Australian parrakeets, which are commonly called love birds. (11) Rather naïvely, perhaps, I thought that since these birds so readily pair off, perhaps two might learn to run a simple maze more rapidly than a single individual would. This turned out to be entirely a mistaken idea. I shall spare you the details concerning this maze; it was adequate in size, so that two birds could pass through practically abreast. Almost all the ninety-odd birds that were tested learned easily to run the maze and normally reduced their time per trial from about two minutes to a few seconds, after six or seven days of training. Errors also were reduced, and several of the birds were trained so that they ran the maze day after day with no errors at all.

The selected summarizing graphs (Figures 29 and 30) will outline the results obtained. It made no difference whether the birds were caged in pairs or separately; if placed alone in the maze the performance was similar. If, however, two birds were put together in the maze, the speed was reduced and errors increased as compared with the scores made by isolated parrakeets. It made no difference whether two males, two females or a male and a female were trained in the maze together; there was always interference. The tendency was for the more rapid

bird to slow down rather than for the slower bird to speed up. The paired birds tended to take the same time and to make the same errors. Given sufficient training, they might make perfect scores so

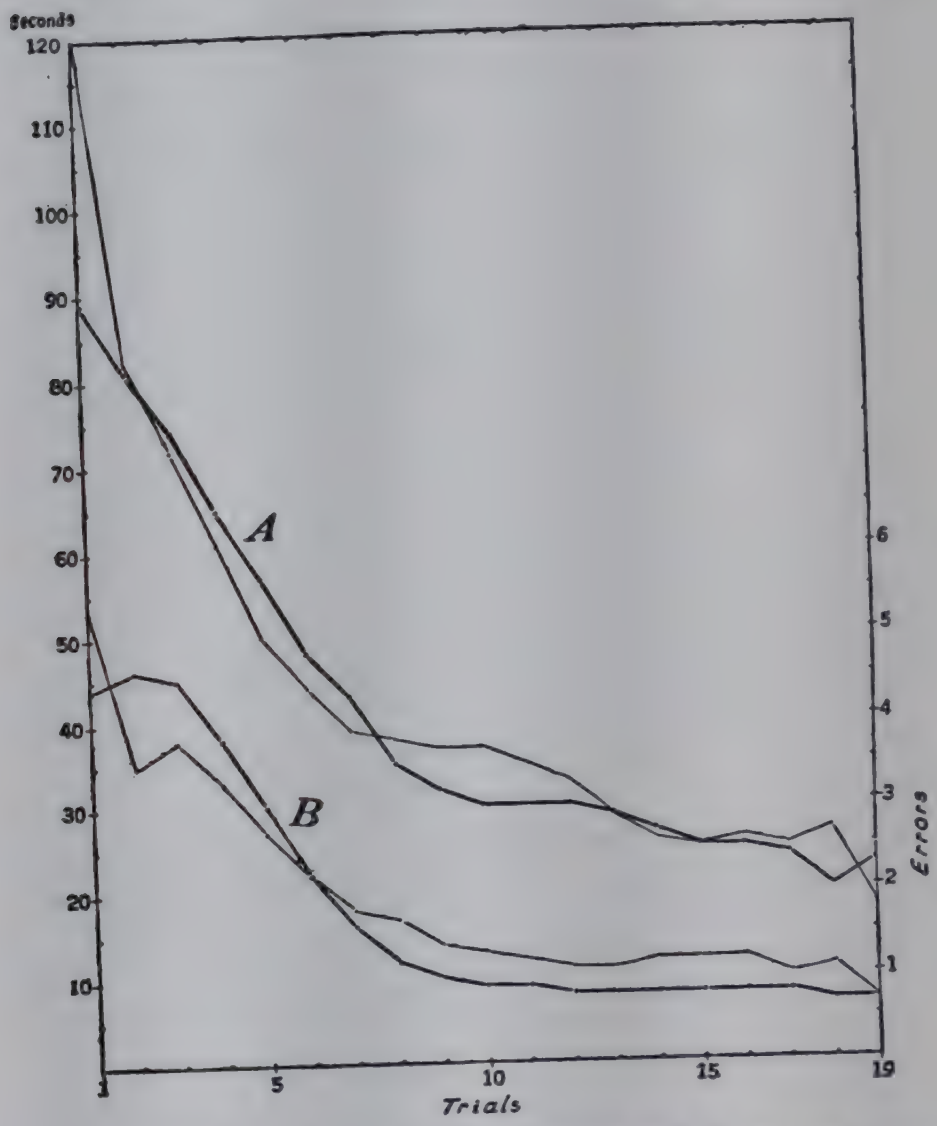


FIG. 29. Parrakeets learn equally well if trained when isolated, whether they are caged singly or in pairs. A, time per trial; B, errors per trial.

far as errors were concerned, but even after long training the performance of pairs was always more

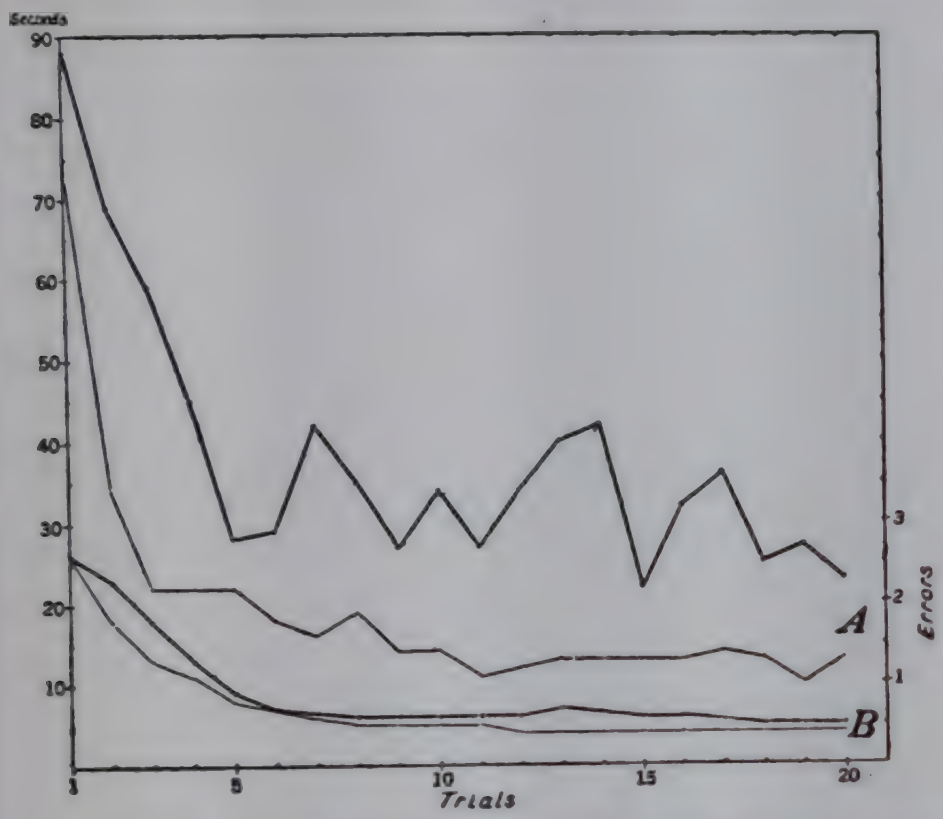


FIG. 30. Parrakeets learn more rapidly if trained alone than if two are placed together in the maze. A, time per trial; B, errors per trial. (The upper curve is unsmoothed; the lower three have been smoothed mathematically.)

erratic than that of isolated birds. When birds that had been trained to a consistent level of excellence were exchanged so that those formerly isolated were paired and those formerly paired were isolated, their behavior in the maze took on the characteristics

usually shown by paired and by isolated birds, proving that the type of reaction given was a result of the numbers present rather than of the working of other factors. With these love birds then, contrary to the original assumption, all indications were that being paired in the maze slowed down the rate of learning and increased the erratic character of their behavior.

Our experience with the general problem did not end here. I teach at the University of Chicago a favorite course called Animal Behavior. In this class the beginning research students attempt some small problem and frequently make good progress toward its superficial solution. One of these student projects has been the training of the common mud-minnow to react to traffic lights. The fish were trained to jump out of water and obtain a bit of earthworm when red was flashed. Under the green light they were conditioned to retire to one of the bottom corners. If they did jump under green light they were fed filter paper soaked in turpentine. Within two months a lot of fishes, isolated one in each small aquarium, could be trained so that they would have been given an A for the project if they had been properly enrolled students.

When, however, several fishes were placed together in the same aquarium and an attempt was made to

train all at the same time the rate of learning was retarded. Paired fish reacted as well as if they had been isolated, but the reactions of groups of four were slowed down, and those of ten even more so. Two fish would rarely jump at once, and when some one individual was getting set to jump for the food under the red light, another would frequently come along and give him a jab in the belly which would stop all tendency to jump for the time.

One more instance remains to be reported. Dr. Welty, who has been mentioned before, undertook to train goldfish to move forward from the rear screened-off portion of an aquarium through a door into a small forward chamber where each was fed just after it came through the opening. (118) An aquarium-maze, similar to those used, is shown in Figure 31. The signal to the fish that it was time to react came from increasing the intensity of light in the aquarium and opening the door between the two compartments. Under Dr. Welty's careful coaching the fish improved rapidly in their speed of reaction and usually had reached a good level of performance by the sixth day of training.

In his experiments almost a thousand fishes were trained at one time or another. The results of a sample experiment are recorded in Figure 32. In this test there were eight goldfish, each isolated in indi-

vidual aquaria, four sets of paired goldfish, two lots of four placed together, and one group of eight in one aquarium. As shown by the graph, there was a

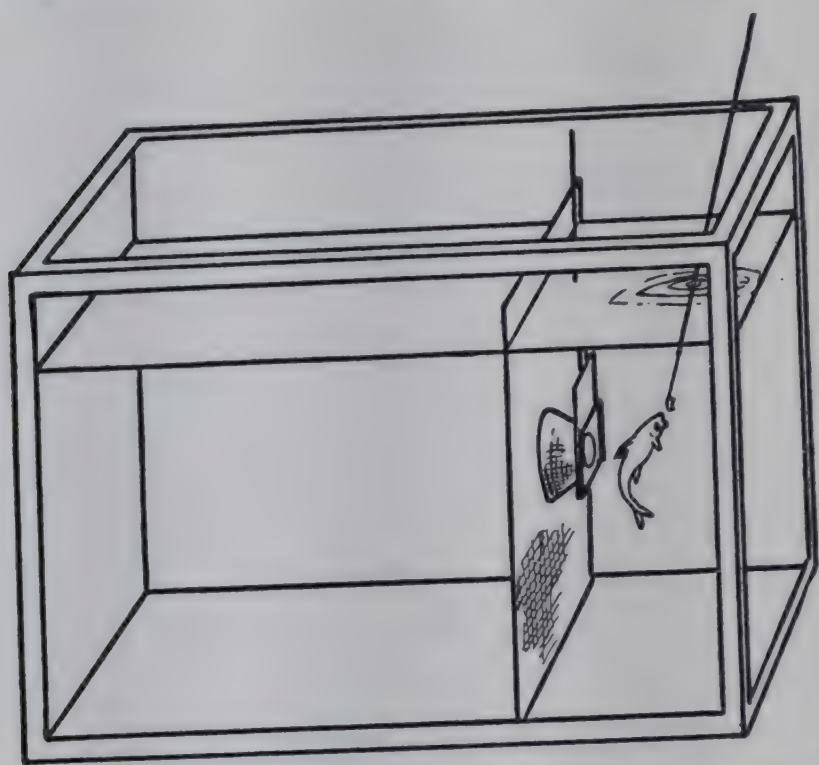


FIG. 31. Feeding a fish which has just come through the opening from the larger side of the aquarium. (From Welty.)

marked group effect on the rate of learning. The speed of first performance of the untrained fishes was most rapid with eight present and slowest with isolated goldfish. In the early days of rapid learning the same order held. This experiment was repeated several times with identical results. Under these conditions there seems to be little doubt but that the

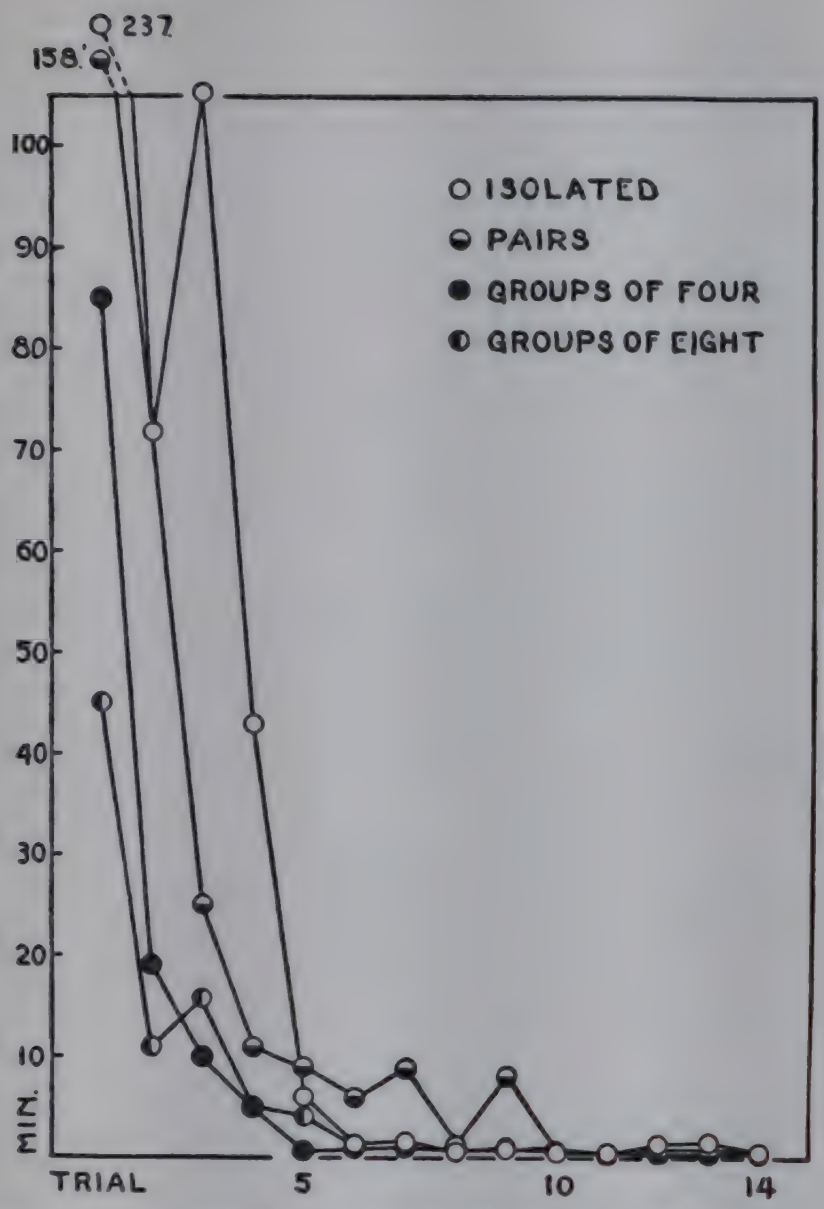


FIG. 32. Goldfish learn to swim a simple aquarium-maze the more readily the more fish there are present. (From Welty.)

groups of goldfish learned to move forward and secure food more rapidly than the same number of isolated fish.

The conditions of the experiments allow certain

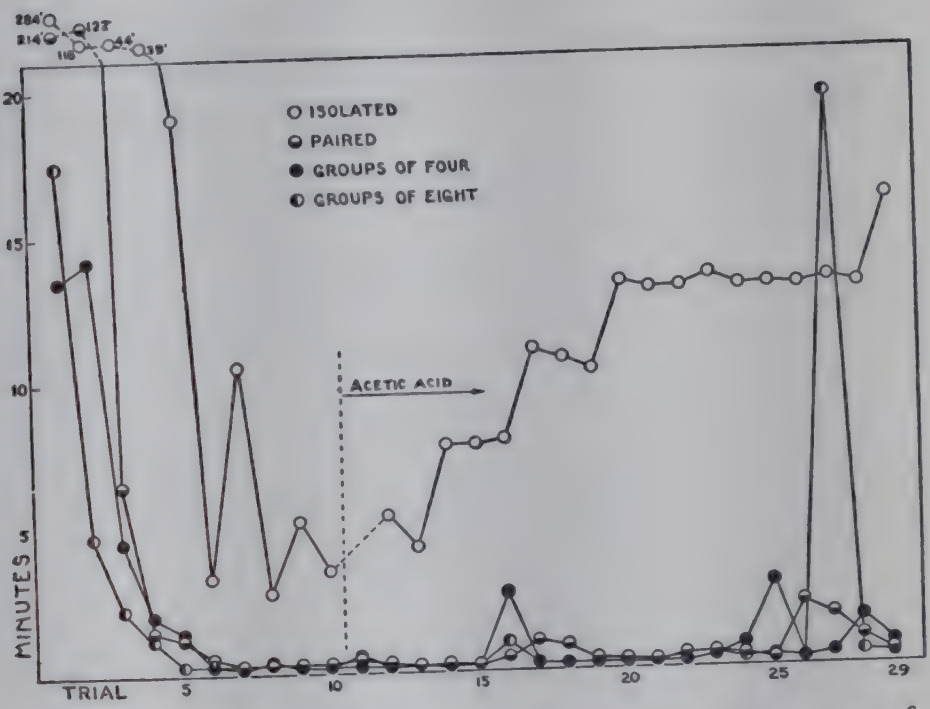


FIG. 33. Isolated goldfish learn the problem set for them less rapidly, and unlearn it more readily. (From Welty.)

types of analyses to be made. One of these is to test the tenacity with which the newly acquired habit will be retained. A set of fish was trained as usual (Figure 33). After ten days, when the grouped fish had been letter-perfect for four days, although the isolated goldfish were still taking some three minutes per trial, the experiment was changed; when-

ever the fish came forward through the gate they were offered pieces of worm soaked in acetic acid. The isolated fish, perhaps because they had not learned to perform so well, perhaps because they were isolated or for some other reason, ceased to react rapidly, and on the twenty-ninth day they were averaging fifteen minutes per trial. The grouped fish were much more steady in behavior, and persisted in coming forward with relatively little change until the twenty-seventh day; and even then the old conditioning held for most of the fish most of the time. Many individuals persisted in coming forward through the gate for a long time after they ceased biting or even swimming toward the acid-treated worm.

When a group of fish are reacting together, if a given individual moves forward through the gate to the feeding space, others may follow because of a group cohesion. It is obvious that if a fish is isolated and moves forward, the faster reaction cannot affect the behavior of other isolated fish.

With this in mind, Dr. Welty undertook a series of experiments in which there were two partitions in the aquarium, with one door opening forward and another door opening through the other partition toward the rear of the aquarium (Figure 34).

The fish were placed in the central space and those in half the tanks were trained to come forward as usual. In the other half, two selected fish were conditioned to come forward and two were similarly

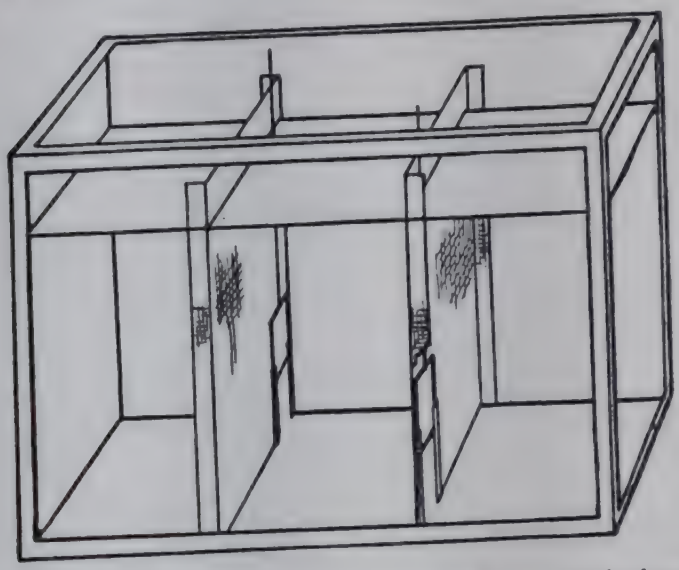


FIG. 34. The aquarium-maze used in training part of the fish to come forward and part to go to the rear to be fed. (From Welty.)

trained to move to the rear compartment to be fed. The experiment was tried several times with goldfish, the minnow, *Fundulus,* common at Woods Hole, and another marine minnow, *Cyprinodon.* For one reason or another, only one series in which the fish were comparable was successfully completed. The results are shown in Figure 35. Generally speaking, the cohering groups of *Cyprinodon* learned more rapidly and reacted more steadily than the separating groups. This, then, is one factor that is working,

at least at times, in causing grouped fish to learn more rapidly in a simple aquarium-maze than isolated fishes under similar treatment.

As the goldfish move forward in the usual divided

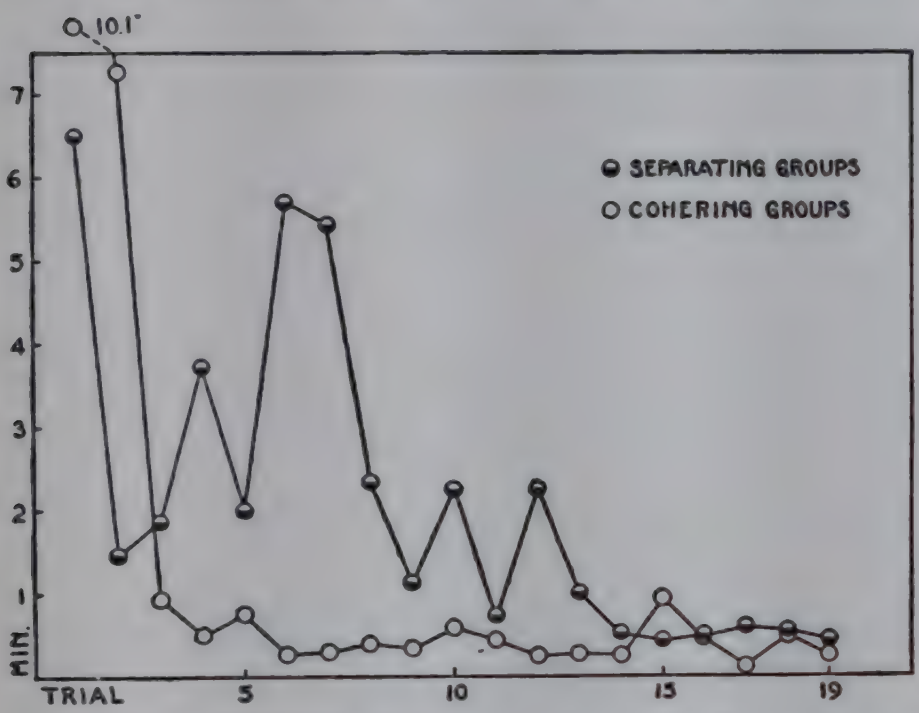


FIG. 35. *Cyprinodon* learn to move in a body more readily than to split into two separate groups. (From Welty.)

aquarium there comes a time when one or more fish may be in front of the screen, and the others in the rear of this advance guard. It was obviously a part of the investigation to find the effect these more rapidly reacting fish had upon their fellows merely as a result of being in the forward chamber. Conceivably they may have served as a lure. Another pos-

sibility is that a rapidly learning individual becomes a leader in the reaction of the whole group.

Both of these possibilities were tested experi-

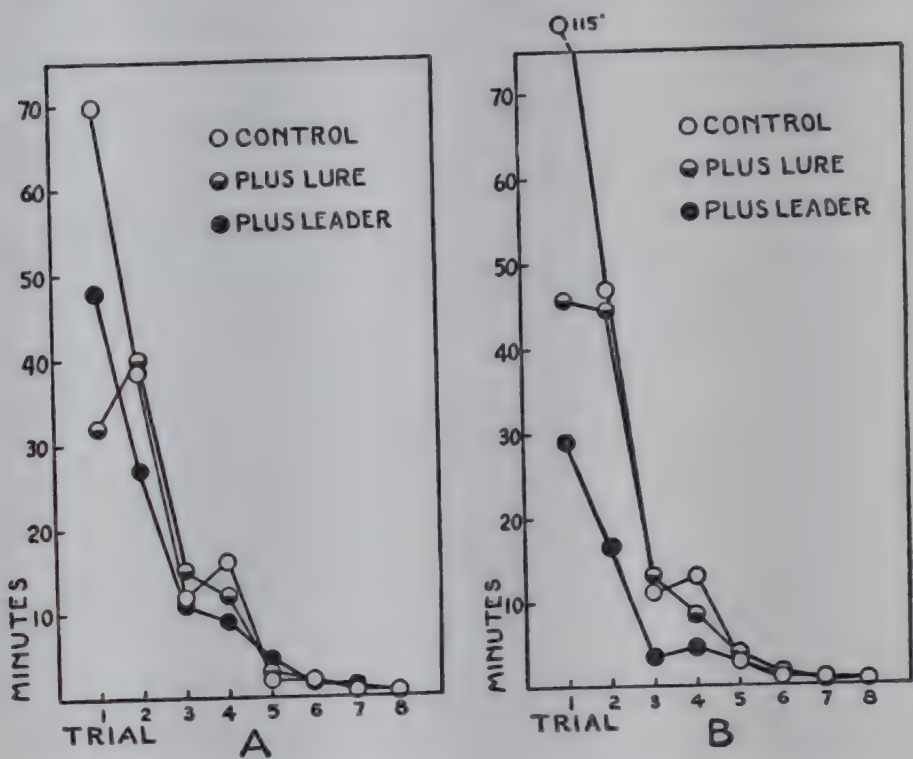


FIG. 36. Goldfish learn more readily if accompanied by a trained leader than if there is a fish in the proper position to act as lure. (From Welty.)

mentally by Dr. Welty, with results which are summarized in Figure 36. Three sets of aquaria were established. In the control aquaria all the goldfish, of which there were four in each tank, were fish which had had no previous experience in these experiments. These were trained as usual. In another set, an untrained fish was kept in each forward com-

partment as a lure and four untrained fish were placed in the rear compartment. These fish were trained as usual; the so-called lure-fish was fed after the first of the untrained lot came through the gateway. In the final set of aquaria a trained fish was introduced along with the four untrained fish. When the light was admitted and the gate was raised this trained fish moved forward, came through the gateway, and was fed immediately. The others followed. As the graphs show, after the first day there was little difference in the reactions given by the control fish and by those which had a lure-fish in front of the screen. The fish with a trained leader generally gave more rapid reactions than either of the others.

There is always a temptation to make comparisons between the learning behavior of these laboratory animals and that of men. Direct comparisons should usually be avoided. However, in human terms, the goldfish reacted more rapidly in the presence of a trained leader which went through the whole behavior process with them, than they did to the presence of one of their kind as a lure-fish in the forward compartment, a sort of signpost to proper behavior. Evidently leaders working with these goldfish can influence them more than fish which by their position merely show them where they can come. It seems fair to say that with these fish demonstration

teaching is the most effective method yet discovered.

Still another attempt was made to study group cohesion in these goldfish. For this purpose aquaria

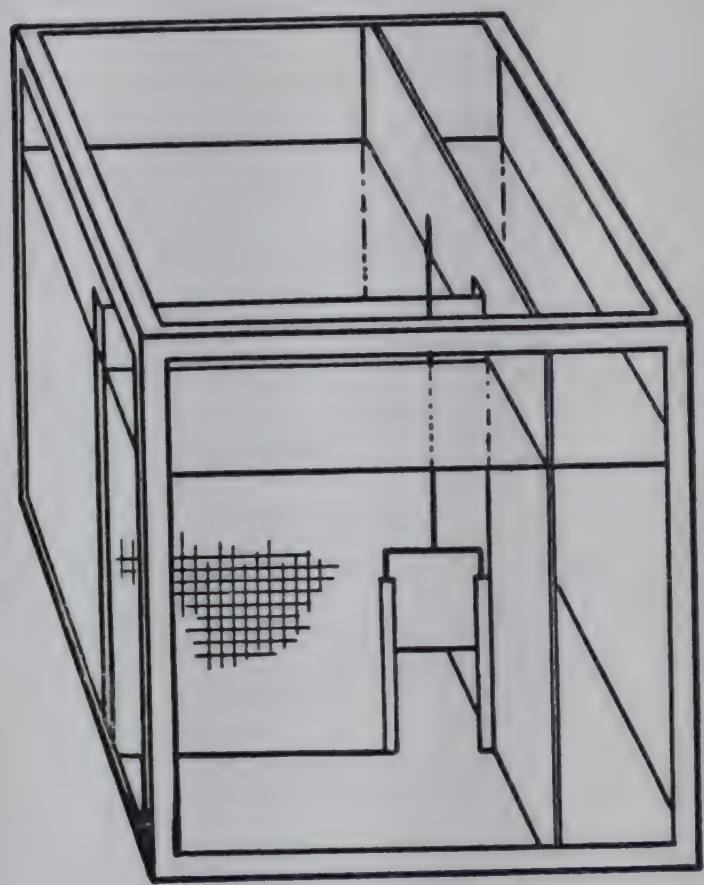


FIG. 37. An aquarium-maze arranged to test the power of observation of fish placed in the side compartment. (From Welty.)

were arranged like those in Figure 37. At the side of the usual aquarium-maze a narrow runway was placed into which untrained goldfish were introduced. In half of the tanks the glass partition was clear and allowed the fish to see the reaction of those

in the larger aquarium-maze. In the other half, the partition was of opaque glass, cutting off the view.

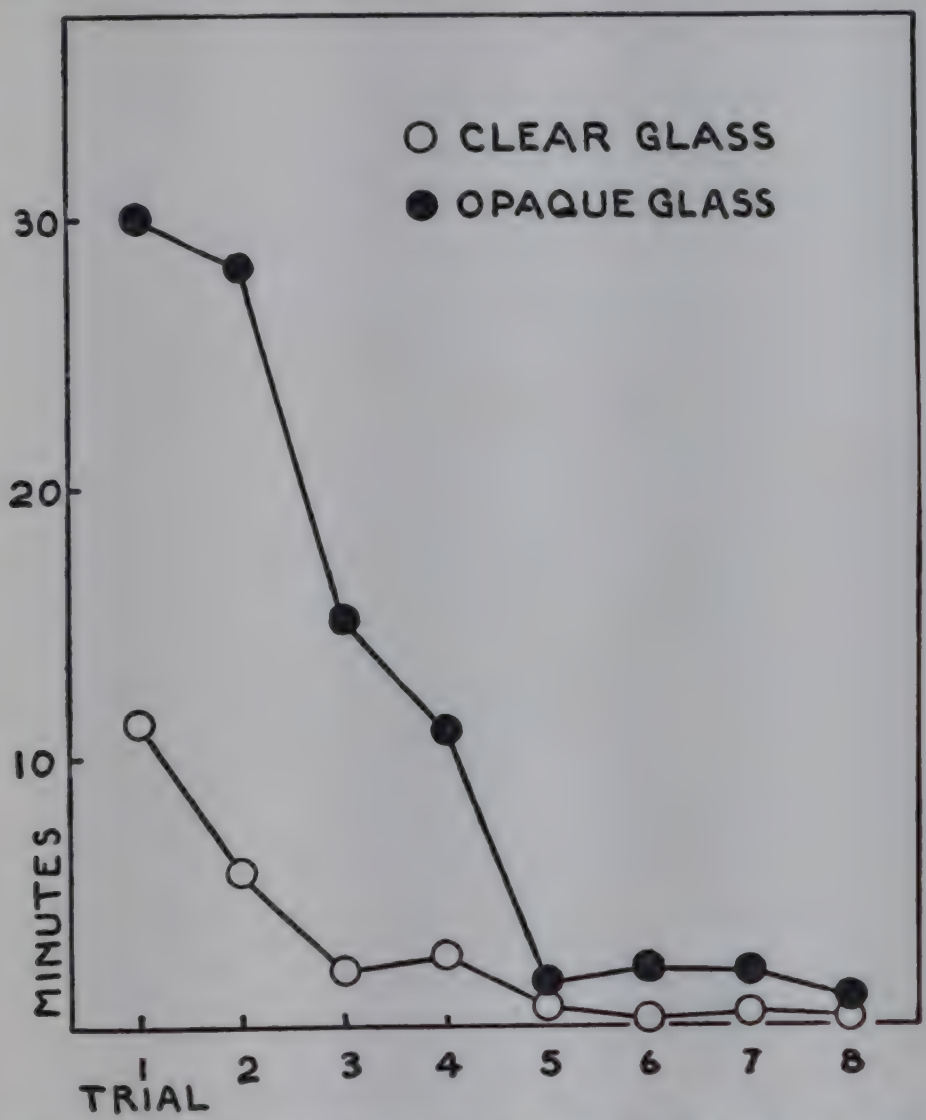


FIG. 38. Goldfish react more rapidly if allowed to watch others perform. (From Welty.)

Trained fish were placed in the aquarium-maze and were run through their performance from ten to twenty times in different experiments. The same

treatment was given the fish in the aquaria with opaque partitions and those with clear glass. The trained fish were then removed and those from the small side chamber were gently transferred to the larger side. An hour later they were given an ordinary test such as had been given to the trained fish. As is clearly shown by the graphs in Figure 38, the fish which had been able to watch the others react behaved decidedly more like trained fish than those which had not been able to see their fellows perform.

As a final check, the whole test was repeated, except that no fish were placed in the larger side of the aquarium. Fifteen times each aquarium was lighted up, the door opened, and the experimenter stood ready to feed any imaginary fish that might come through. Then when those in the side passages were transferred, there was no essential difference in the behavior of the fish from the two types of aquaria, and the experimenter was free from any suggestion that he might have been signaling the fish.

The results of these experiments suggest that there is such a thing as imitation among goldfish. Whether there is or not depends, as Dr. Welty rightly says, largely upon the definition given to the word imitation. These fish probably do imitate each other on a relatively simple instinctive level. The untrained fish that watched the reaction of their trained fel-

lows through the clear glass became conditioned in two ways which were not open to the fish behind an opaque glass. In the first place they saw the fish move forward on the reception of a given stimulus, pass through the gate, receive food, and give no evidence of an avoiding or "fright" reaction. This probably gave what might be called a certain reassurance. Secondly, they showed group cohesion, and moved forward with the reacting fishes; at times they were even seen to move forward in advance of the fishes on the maze side of the aquarium.

When transferred to the aquarium-maze and given the releasing stimulus of an increase in light, accompanied by the opening of the gate, both types of previous experience probably played a role in producing a faster reaction. Fish behind the opaque glass could have neither of these helpful experiences. When their narrow aquarium was flooded with light they ordinarily moved back to the far end and remained there. There was nothing to train them to overcome this normally negative reaction. So reviewed, it must be said that this behavior has some points of resemblance to what is called imitation in other animals.

There is also an element of imitation in the greater food consumption of grouped fishes. One fish sees another pursue, attack and consume a bit of

food and its own feeding mechanism is set off as a result of this visual experience, even though its own hunger might not have been sufficient to stimulate feeding behavior. It is difficult to say to what extent such behavior is an expression of competition as contrasted with unconscious co-operation. The two types of motivation overlap here and elsewhere.

The evidence which we have been considering furthers our understanding of the fundamental nature of group activities among many animals, some of which are not usually regarded as being truly social. The whole emphasis of this chapter has been laid upon facilitation as the result of greater numbers being present. This kind of social facilitation has been described for such diverse processes as breeding behavior, eating, working and learning.

Added numbers do not always facilitate these activities, as was shown by the analyses of the effect of numbers upon the rate of learning. With some animals, for example men and goldfish, under certain situations, learning is more rapid with several present; but with others, such as parrakeets and mudminnows, under the conditions tested, increased numbers lead to a lower rate of learning. It seems that no all-inclusive positive statement can as yet be made in this field. One can, however, make the affirmation that in the general realm here considered the pres-

ence of additional numbers by no means always retards, and is frequently stimulating. As before with regard to other processes, we find that in certain cases there are ill effects of undercrowding as well as ill effects of overcrowding. Without careful experimental exploration, we cannot predict which effect will emerge from a given situation.

One other result comes from these studies which will help us to clarify evidence still to be presented, as well as to review that already given. We have come upon another measure of the existence of social behavior. Reactions may be regarded as social in nature to the extent that they differ from those that would be given if the animals were alone. Such differences are frequently quantitative, as they have been in the cases we have discussed, although qualitative differences occur as a result of a change in the numbers present.

From this point of view social behavior may have or may lack positive survival value. All that is necessary is that the behavior be different from that which would be given if the animal were solitary. In this sense all the animals whose behavior we have been discussing are social to a considerable degree; the more so, the greater the difference between their behavior when grouped and when isolated.

When the behavior of such animals as cockroaches,

fishes, birds and rats shows evidence of distinct modification as a result of more than one being present, we have another suggestion that there exists a broad substratum of partially social behavior. There are many indications that this extends through the whole animal kingdom. From such a substratum, given suitable conditions, societies emerge now and again as they have among ants and men. At these higher social levels, as is to be expected, the type of behavior shown under many conditions is related even more closely to the number of animals present than with less social cockroaches and fish.

VI. Group Organization

WE ALL know that human society is more or less closely organized. Sometimes, as in military circles, some business organizations, and certain universities, there is a line organization which extends in a definite order, step by step from the highest official to the lowest rank. Frequently, however, the organization is more complex, intricate and temporary.

We have known for some time, too, that in herds of the larger mammals, where one can distinguish different individuals, the group may be organized to some extent with a dominant leader and frequently with sub-leaders that stand out above the common run of the herd. (16)

Despite this knowledge we have found with surprise that other animal groups, a flock of birds for example, in which the different birds are indistinguishable to the human eye, also are organized into a social hierarchy, frequently with a well-recognized social order which runs through the entire flock. The situation that has been revealed in these flocks

of birds is amusing, interesting and important enough to warrant more attention than it is receiving at present.

Studies of the sort I am going to describe were initiated by a Norwegian named Schjelderup-Ebbe. (108) They were made possible by the use of colored leg bands and other markings by which the different individuals could be recognized by a human observer. Apparently the birds themselves knew the individual members of the flock without such artificial aids.

Not because it is the most important work on the subject, but because I can best vouch for it in detail and in general, I shall present certain analyses of group organizations that have been made in our own laboratory.

The organization of flocks of chickens is fairly firmly fixed. This is particularly the case with hens. The social order is indicated by the giving and receiving of pecks, or by reaction to threats of pecking; and hence the social hierarchy among birds is frequently referred to as the peck-order.

When two chickens meet for the first time there is either a fight or one gives way without fighting. If one of the two is immature while the other is fully developed, the older bird usually dominates. Thereafter when these two meet the one which has

acquired the peck-right, that is, the right to peck another without being pecked in return, exercises it except in the event of a successful revolt which, with chickens, rarely occurs.

The intensity of pair contact-reactions varies greatly. A superior may peck a subordinate severely, or lightly, or it may only threaten to do so. It usually turns its head, points its bill toward the subordinate and takes a few steps in that direction. It may then give a low deep characteristic sound which frequently accompanies an actual peck, and stretch its neck up and out without the resulting peck which it seems just ready to administer.

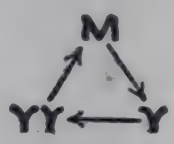
The peck, when actually delivered, may be light, heavy, or slashing. These vigorous pecks may be painful even to man, as anyone can testify who has tried to take a setting hen off her nest; and particularly painful if repeated in the same spot. The pecking bird may draw blood from the comb or may pull feathers from the neck of the pecked fowl. The peck is frequently aimed at the comb or the top of the head; often it is not received with full force, for the pecked bird dodges. Less often the peck is directed toward back or shoulders.

The severity of a peck which lands as aimed is illustrated by a recent observation in one of our small flocks. One bird received a vicious peck di-

rectly on the top of its head; it walked backward two or three feet, staggered and fell, arose and again walked backward in a blind course that took it into the bird that had given the original peck. By that

RW	pecks all	12	: A, BG, BB, M, Y, YY, BG_2, GR, R, GY, RY, RR.
RR	pecks	11	: A, BG, BB, M, Y, YY, BG_2, GR, R, GY, RY.
RY	pecks	10	: A, BG, BB, M, Y, YY, BG_2, GR, R, GY.
GY	pecks	9	: A, BG, BB, M, Y, YY, BG_2, GR, R.
R	pecks	8	: A, BG, BB, M, Y, YY, BG_2, GR.
GR	pecks	7	: A, BG, BB, M, Y, YY, BG_2.
BG_2	pecks	6	: A, BG, BB, M, Y, YY.

YY	pecks	4	: A, BG, BB, M.
M	pecks	4	: A, BG, BB, Y.
Y	pecks	4	: A, BG, BB, YY.



BB	pecks	2	: A, BG.
BG	pecks	1	: A.
A	pecks	0	

FIG. 39. Flocks of hens are organized into a definite social hierarchy.

time the aggressor had turned to eating and paid no attention to this chance contact.

As a result of patient watching of pecks received and delivered, it is possible to find, with a high degree of accuracy, the social status of birds in a relatively small flock. (80) The organization of one such flock of brown leghorn pullets is shown in Figure 39. This peck-order was determined after sixty days of observation. As shown by the chart, there was a regular line organization down to the eighth bird.

Then a triangle was encountered in which M pecked Y, Y pecked YY and YY pecked M; and each of these had the peck-right over the remaining members of the flock.

Such irregularities are by no means uncommon even in well-established flocks. A hen which is otherwise the *alpha* bird in the pen may be pecked with impunity by some low-ranking member, although the latter is in turn pecked by many birds over which the *alpha* hen has a clearly established social superiority. This inconsistency may result from the low-ranking bird having first met the *alpha* bird on one of its off days, gained the advantage in the first combat and managed to keep it thereafter with the aid of the psychological dominance thus established.

Similar social hierarchies exist also among flocks of male birds. One flock of cockerels, which we studied for seventy days, demonstrated the social order shown in Figure 40 in which there are six triangle situations that run through all the upper part of the social scale, but are especially evident in the middle ranks where B is involved in four of them.

Cockerels are more pugnacious than pullets, even when they are kept, as these were, on a diet which somewhat restricts the tendency to fight. There were

more revolts and these were more likely to be successful. For example, in this flock of cockerels, the four birds lettered in bold-faced type in Figure 40 showed reversals, and with some the social rank had

BW	pecks 9:	W,	BY,	G,	RY,	B,	BG,	Y,	R,	GY.		
BR	pecks 8:	W,	BY,	G,	RY,		BG,	Y,	**R,**		BW.	
GY	pecks 8:	**W,**	BY,	G,	RY,	B,	**BG,**	Y,				BR.
R	pecks 7:	W,	*BY,*	**G,**	RY,	B,	BG,			GY.		
Y	pecks 6:	W,	BY,	G,	RY,		BG,		R.			
GB	pecks 5:	W,	BY,	G,	RY,	B.						
B	pecks 4:	W,		G,	RY,			Y.				
RY	pecks 3:	W,	BY,	G.								
G	pecks 2:	W,	*BY.*									
BY	pecks 2:	W,				B.						
W	pecks 0.											

In this order there are six triangle situations as follows:

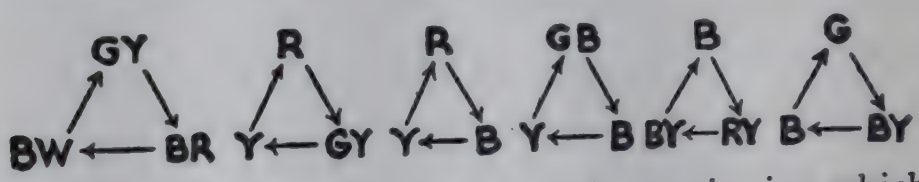


FIG. 40. Cockerels also have a social organization which is, however, somewhat more confused than with hens.

not been finally determined even after seventy days of observations. Thus BY was observed to peck G on six occasions, while G pecked BY eight times. Ideally, in work of this kind, the birds should be kept under observation throughout their waking hours in order that we may have the full history of their behavior. Such prolonged watching is impracticable, particularly since during much of the day there is little pecking. Actually, observations were

restricted to the time near feeding, when the birds were most likely to fight. Taken together with the greater number of triangles, the reversals indicate a less stable social order among these male birds than among their sisters.

For a time there was no completely dominant bird among the cockerels. BW, which stood highest in general, was pecked by BR, which ranked otherwise just below him. One day BR and Y started to fight, as they had done many times before, with BR winning. This time Y struck through to the eye, which closed as a result, and BR retreated. The injury was such that the tender-hearted observer thought that BR needed special treatment, and removed him to a hospital pen. The eye healed, and two weeks later the recovered bird was returned to the flock which he had almost dominated. In these two weeks of absence he had lost his social status entirely, and was pecked even by W, which had not been seen before to peck a fellow cockerel. The reason for his loss of position is not clear. He had been severely injured, he had lost a fight to an inferior, and he had been absent from the flock for fourteen days. For one or all of these reasons he had lost caste so completely that five days later he had to be removed from the flock, literally to save his life.

During the five days that BR was again with the

flock, he avoided contacts with others as much as possible, and spent a great deal of his time crowding under a low shelf on which the water dish was kept. In our experience, the lowest ranking chicken in a flock tends to avoid social contacts as BR did after his fall from superior position. Frequently the low-ranking birds show many objective signs of fear. They spend time in out-of-the-way places, feed after others have fed, and make their way around cautiously, apparently with an eye out to avoid contacts. The lowest ranking birds may appear lean, and their plumage is somewhat more rumpled because they have less time to arrange it. Dominant birds, on the other hand, are characterized by a complete absence of signs of fear or of any attempt to avoid birds of lower ranks. Some birds, usually those high in the peck-order but not at the top of it, show few avoiding reactions to their superiors, and, when pecked, apparently take it lightly and pass on.

Chickens show some other interesting reactions which are related to their position in the social hierarchy to which they belong. Professor Murchison, a psychologist at Clark University, has reported studies on the behavior of a flock of six cocks and five pullets. (83) In one series of experiments pair after pair of the cocks were selected at random and placed at either end of a narrow runway behind

glass doors which allowed them full sight of each other. When the glass doors were opened the cocks ran toward each other. The point of meeting was proportional to the relative position of the two in the social scale, for the more dominant bird traveled farther than the subordinate one.

In another experiment two cocks were placed in small wire cages in which they were plainly visible, and these cages were set in an enclosure about six feet apart. If a third male from the flock were introduced into the pen the free bird would go toward the caged cock which was relatively lower in the social scale. In this it behaved exactly opposite to the females which were members of the same flock and "acquainted" with both roosters. A hen released under similar conditions is said to make her way toward the cock that has the higher social position.

In our studies we have usually found that the birds higher in the social order had more social contacts than those that were at the bottom of the peck-order. The correlation is not always exact, but to date we have found few exceptions to the rule that the bird lowest in the peck-order has the fewest contacts. A quantitative difference, closely associated with social rank, may be found in the number of pecks delivered when there is no difference in the total contacts among the upper birds. In a recent

study (9) in which four pens were under observation with five or six pullets in each, out of 4,400 pecks the ranking birds gave 1,800, the second in the lists gave 1,092, and so on in regularly declining numbers until those next to the bottom gave 136 and the birds that were lowest in their respective flocks gave none at all.

Murchison has reported a variation of this general rule. In studying the sexual behavior of his birds, of the three cocks that gave the mating reaction the number of treadings stood in direct relation to social position, with the ranking cock treading pullets most frequently. Interestingly enough, the top pullet was also the bird which mated most frequently, and the number of matings of the remaining females was in direct proportion to their social position. This appears to be a special case of the general rule that birds high in the peck-order have more social contacts than those that are low in social rank.

These are some of the known relationships existing among birds that have a relatively fixed group organization. Schjelderup-Ebbe, (109, 110) who has made observations on over fifty species of birds, including, besides the common chicken, a sparrow, various ducks, geese, pheasants, cockatoos, parrots, and the common caged canary, is convinced that despotism is one of the major biological principles;

that whenever two birds are together invariably one is despot and the other subservient and both know it. He has said, "Despotism is the basic idea of the world, indissolubly bound up with all life and existence. On it rests the meaning of the struggle for existence." He applies this principle to interactions of men and of other animals and even to lifeless things. He says: "There is nothing that does not have a despot . . . usually a great number of despots. The storm is despot over the water; the lightning over the rock; water over the stone which it dissolves"; and he cites with approval the old German proverb that God is despot over the Devil.

This poetry of Schjelderup-Ebbe's is striking, but does it rightly interpret the facts? We have spent a considerable amount of time at Chicago, investigating the social order of various birds. Messrs. Masure, Shoemaker, Collias and Kellogg and Miss Bennett have been particularly active in this work. We have not yet studied as many varieties of birds as Schjelderup-Ebbe, and we have no experience to report about the relation between God and the Devil. Of the birds we have studied, only the flocks of white-throated sparrows approach the common chickens in the fixity of their social hierarchies, and they do not equal it. The common pigeon, the ring dove, the common canary and parrakeets show a less

rigid type of social organization which I can illustrate by explaining the situation as we have found it among common pigeons. (80)

The observations were made on a group of fourteen white king pigeons, half of which were male and half female. Their social order was observed in sex-segregated flocks until, after a month, it seemed to be fairly stable; then the flocks were combined, and after a month during which five of the seven possible pairs mated, the sexes were again segregated for twenty-eight days of further study. The results are essentially similar both for the males and the females for the period when the sexes were separate, so that I shall follow only the reactions of the female flock. The essential facts can be described with the aid of the diagrams in Figure 41. These show the social interactions between the females lowest in the social order.

Let us examine Chart A with some care. This charts the relationships of the five birds that were lowest in the pre-mating flock. All these were dominated in the main by BY and BB. The figures show that BR was seen to peck GW ten times and was pecked by GW, and retreated from her nine times. GW pecked BW thirteen times, but lost in four encounters. BR won ten and lost seven of its observed contacts with BW, which won thirteen and

lost ten with RY. RY in turn was practically even (eight to seven) with BR and slightly ahead in its relations with GW and RW. I do not intend to sug-

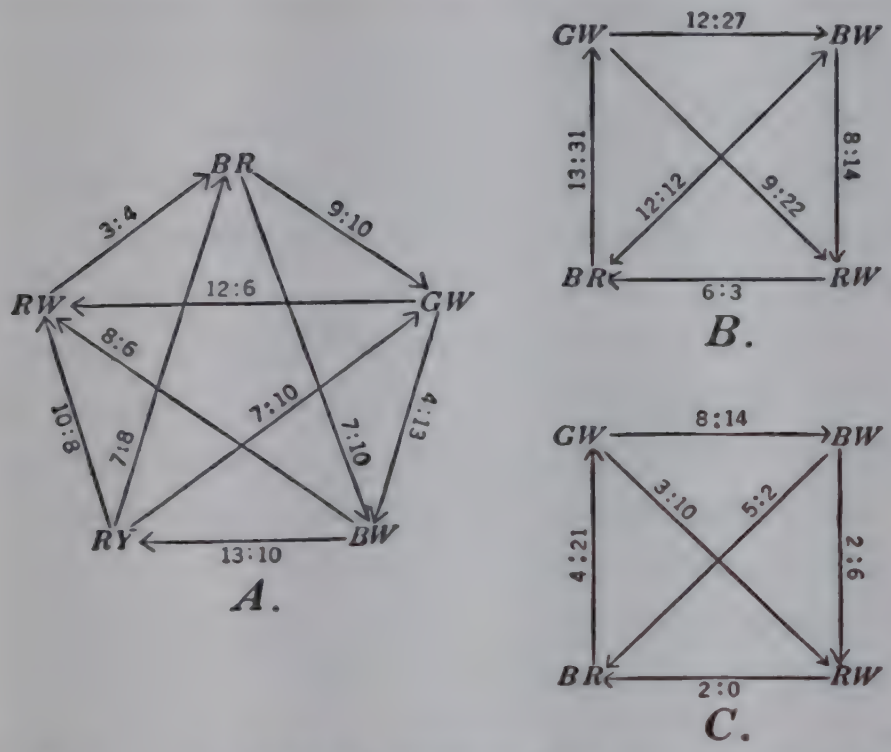


FIG. 41. In flocks of pigeons the organization is one of peck-dominance rather than of peck-right. The pigeons highest in the social order are omitted from these diagrams. A, the pre-mating flock; B, the entire period of observation; C, the post-mating flock.

gest that most of these differences are important; in fact that is the point. With flocks which are organized as are these pigeons, it frequently becomes difficult to decide which bird stands higher in the social order.

It is important to note that in none of these cases,

in fact in only one of all the different reaction pairs whose behavior is summarized in these charts, was there an absolute dominance of one bird by the other, and then only two contact reactions were seen. When all contacts throughout the whole period of observation are considered, there was at least one time for each of the contact pairs when the bird which usually lost out dominated the contact reaction.

In Chart B, which shows all the reactions during pre- and post-mating, and in C which records the contacts for the post-mating season only, the four birds represented by the diagrams were dominated by three others, RY, BY and BB. It is worth emphasizing that with these birds an absolute despotism was not established. Even RY, which more than any other bird dominated the post-mating flock, lost contact reactions to each of the others except to RW, which was lowest of all. While it was winning 329 reactions it lost 58, and each of the other females, RW excepted, dominated it at least three times in the post-mating observations.

The picture that emerges is one of a flock which is organized into a social hierarchy, but one which is not so hard and fast as that found with chickens. In the long run one becomes fairly sure which bird in each of the groups will dominate in the larger

number of their contacts, but the result of the next meeting between two individuals is not to be known with certainty until it has taken place. Within the same hour and even within a few minutes reversals in dominance may take place without anything unusual in the circumstances.

Putting the matter somewhat facetiously, chickens appear to have developed the sort of "line organization" characteristic of a military system or a fascist state, while these pigeons, together with the ring doves, canaries and parrakeets, are more democratic. The social hierarchy among chickens is based on an almost absolute peck-right which smacks strongly of the despotism of which Schjelderup-Ebbe writes, while these other birds have an organization based on peck-dominance rather than on absolute peck-right.

With such birds social position is not fixed once and for all. Consider the case of RY among pigeons. When results were first thrown together at the end of two weeks of observation, RY was at the bottom of the flock, a position which it retained for twelve more days. Then something began to happen. What it was, I wish I knew. RY began to go up in her social world. After six days she ranked a shaky third, clearly dominated on the average by BY and BB.

Then the pigeons were allowed to mate. During

the mating period BY, which was top bird in the pre-mating flock of females, and RY did not pair off with any of the males. Again I do not know why. After the experiment was finished RY was carefully autopsied and we could find no evidence of anything physically abnormal. When the sexes were again segregated RY was the top-ranking bird among her fellow females, and remained so. She was seen to have 101 contacts with BY, the former *alpha* bird, and to win 83 of them; she had 77 observed contacts with BB, which had formerly been second from the top, and defeated her 53 times. In the pre-mating period RY lost two combats for each that she won; in the post-mating flock she won five contacts for each that was lost.

This raises in a rather dramatic fashion questions as to what qualities make for a dominant bird. This problem is not yet solved. With these birds, social rank is in part a matter of seniority. Mature chickens usually dominate immature ones and maintain their dominance long after the former youngsters have become fully mature and possibly physically able to displace the senior members. This is good evidence that memory of former defeats plays a role in maintaining the social order once it is established. When chickens strange to each other are put together for the first time dominance usually goes to the bird

with superior fighting or bluffing ability. Maturity, strength, courage, pugnacity and health, all seem essential qualities making for dominance among chickens. Luck of combat also seems to play a part when one considers the numerous triangle situations that have been discovered. Since cockerels have certain of these qualities more than pullets, a male bird, if present, dominates a flock of hens.

There seems to be little if any correlation between greater weight and position in the peck-order. The location of the combat seems to be important. Schjelderup-Ebbe found that chickens in their home yard win more combats than strangers to that yard; and Mr. Shoemaker has reported that, with canaries, each bird becomes dominant in the region near its nest. (113) We found some years ago that with pigeons one might be dominant on the ground about the feed pan and another have first rank at the entrance to the roosts. (80)

With chickens, as I have said, the larger, stronger, more pugnacious males usually dominate the females. This is said to be generally true in species in which the male is larger or more showy than the female. With the parrakeets, (11) whose social order in many ways resembles that of pigeons, the females are dominant over the males except in the breeding season. While breeding and nesting are in progress

positions are reversed, and a previously hen-pecked male may drive his usually dominant mate back onto the nest when she attempts to leave it. The sexes in these parrakeets can be told apart only by slight differences in color.

When hens are giving the brooding reaction or are caring for small chickens, they become less submissive to other hens. Some of the other birds, whose social ranking has been investigated, move up and down in the social scale according to the phase of the breeding and nesting cycle which they are in at the time.

It has been reported that with hens those high in the peck-order have a higher IQ than their more lowly placed flock mates. (72) The IQ was measured in this case by placing grains of corn out on the floor with every other grain securely fastened down, and finding the speed and accuracy with which the fowls would learn to peck at the loose grains only.

We have had as yet only the most casual personal contact with this problem so far as chickens are concerned. With the parrakeets, Masure and I could find no evidence of a positive correlation between any aspect of ability to learn a maze and social rank.

From this summary it is evident that in spite of a great deal of study we do not know all the factors which determine the position of birds in their social

order. There is some suggestion from the effect of broodiness in hens and from observations on the nesting cycle in canaries that there may be elements of control by hormones. This lead is being investigated actively at present, but I have no definite results to report. (6)

Some of the complications in determining the factors that make for dominance are shown by the preliminary summary which Mr. Shoemaker has given me of his studies on the social hierarchy in canaries. The space available for the caged flock is a matter of importance. When confined in relatively small space, the social order becomes more simple and definite and there is no complication over the question of territorial rights. With more space, as for example in a large flight cage, individual territories tend to become established in which the particular bird is supreme even though it ranks low in the neutral ground around the bath bowls, the feeding places, or regions where nesting material is stored.

When canaries are allowed to mate and small nesting cages are supplied around the walls of the flight cage, each individual male is master in its own nest cage and controls more or less territory around the cage entrance. Under these conditions even the birds lowest in the social order dominate in some restricted space about their nest.

In general these canaries show more pecking among the males than among the females, and during the nesting period the female does little to defend the nest territory; that is the work of her mate. In this home territory the social dominance of the male over his fellow males is not steady but varies with different phases of the breeding cycle. During the processes of nest-building, egg-laying and incubation, the male tends to become more dominant. This is shown by an increase in the size of the territory about the nest which he dominates, and by the fact that when on neutral territory he tends to win more of his pair contacts. During the rest of the cycle the male tends to lose dominance as measured by both these criteria.

It is worth noting that in the course of these pulsations in dominance the male may not actually move up in the social scale as determined by the number of birds which he fully dominates. He may win more of his individual pair contacts without actually oversetting the usual trend. The same bird may show fluctuations in dominance during the day. Thus one male regularly dominated less territory of an evening than he did in the morning. This may well be a matter of stamina.

In some cases the relation between the sexes in these canaries hinges on another complication. For

example, a female, 15, mated with a male, 55, which stood about midway in the social order among the males: 55 dominated the other females and all the other males dominated over 15. However, of thirty-three observed contacts between 15 and 55, the male lost all but one! The male parrakeet will drive back on her nest the female who has left it, but 55, like other male canaries, coaxed his mate back to her nest with offers of food.

Until studies are further advanced, we cannot be sure how many of these complications which Mr. Shoemaker has recorded for the canaries are found elsewhere even among birds. It seems reasonable to suppose, however, that the social hierarchy is rarely as simple in its organization as a mere listing of the social ranking seems to indicate.

With all these birds, high rank in the social order of the flock means much greater freedom of action, more ready access to food and a generally less strained style of living. It is hard to say whether in nature it means more than this, although it seems probable that in times of food shortage, or other phases of environmental stress, the ranking birds who have the first opportunity at food might readily fare better than those low in the social scale. Fortunately, enough observations have been made in nature so we know that with some species the peck-

order, which has been most studied in restricted cages and pens, does occur in the wild.

The *alpha* bird in a penned flock of chickens does not necessarily lead in foraging expeditions when the flock has more space. Fischel, a German, reports that when hens of known peck-order are released to forage in an orchard the dominant and near-dominant birds may or may not be at the apex of the foraging flock. (46) Usually the leadership changes from time to time and moreover the leading bird seems always more or less dependent upon her followers. If she gets too far out ahead the leader turns back and rejoins the flock or waits for them to catch up. Similar hesitation by the leader when it has advanced some distance in front of its followers has been observed among other animals, notably among ants and men.

This problem of leadership among birds is related to, but not identical with, position in the social order. There are many aspects of the problem into which we cannot go at present, pending a closer and more revealing study than has appeared as yet of the qualities that make for leadership.

With some herds or hordes of mammals leadership rests with an old and experienced female. (16) In such herds the females and young frequently make up the more stable part of the social group,

to which males attach themselves during the mating season. With other mammals the male is the leader, and sometimes a jealous one, that drives other males out of the herd; although in some cases several males are tolerated. (3)

Leadership does not always go to the faster or stronger animal; in fact, the position of being out in front of the flock may not mean real leadership. An interesting example of such pseudo-leadership has been recorded for a mixed group of shore birds observed by Mr. Nichols of the American Museum of Natural History. (85)

He found a mixed flock of such birds which was composed of two young dowitchers, with a dozen black-bellied plovers and a single golden plover. Under these conditions certain of the birds could readily be distinguished from the others. When the flock was flushed, the flight of the golden plover was comparatively rapid and it was soon ahead of all of the rest. The dowitchers were slow and tended to fall behind, and when this happened the black-bellied plover wheeled. This affected both the apparent leader, the golden plover, and the lagging dowitchers. The former, finding itself alone without followers, rose above the flock, took the new direction and dived down with a few swift wing beats, again the apparent leader of them all. The

slower dowitchers took the chord of the arc made by the wheeling flock and so caught up with and again became an integral part of the flying group. Soon again the slow dowitchers lagged and the whole performance was repeated.

These observations do not reveal the stimulus which releases the wheeling mechanism of the main flock. The simplest explanation, that the leader, finding himself out alone in front, starts to turn and so gives a stimulus to the keen-sighted remainder so that they also shift direction almost instantaneously, does not hold in this mixed flock, for the observations indicate clearly that the apparent leader, the golden plover, was following along in front of the main flock as much as the slow dowitchers were following along behind it.

Neither does this simple-leadership sort of explanation fit the facts as observed among wheeling flocks of other shore birds or of pigeons. In such flocks the stimulus to turn frequently seems to originate in one of the flanks, and spreads from that point rapidly through the flock. Here again the apparent leaders may not be the actual ones. It is possible, though we are not yet sure of it, that in such flocks made of birds which we cannot tell apart, the faster individuals also may dive through the flock

to the foremost position, taking their direction from the whole flock.

However the signal for turning originates, the wheeling takes place so rapidly that mythical explanations are still being advanced. I have a small book written on the subject by an English author, called, *Thought-transference (or What) in Birds?* (111) The title correctly summarizes the contents of the book.

I would not have you conclude from my repeated emphasis on the absence of definite leadership in these flocks of birds, and on the presence of a pseudo-leadership when the flock is really determining the direction that is taken by the bird in front, that there is no real leadership among other animals and among men. And I must make it clear that here I am speaking of real leadership and not of a peck-order, which, as is true with social position in human society, does not imply leadership at all. Such a position could not be successfully maintained by a person trained in science rather than in dialectics. But apparently, at least among so-called lower animals, the leader is frequently as dependent on his followers as they are on him, and sometimes even more so. A similar situation occurs in human affairs often enough and under such a variety of situations that the relationship deserves more careful consideration

than it usually receives when problems of leadership are discussed.

While those of us who have been engaged in these studies have probably never been wholly unaware of the possibility of amusing cross-references to man, I must insist that our motivation has not been that of making an oblique attack upon human social relations. Rather, we have found problems concerned with the social organization of birds and other animals interesting and important on their own account.

We have, of course, a feeling that different animals have much in common in group psychology and in sociology, as well as in more distinctly physiological processes. It is the viewpoint of general physiology that we cannot understand the working and the possibilities of the human nervous system, for example, without study of the functioning of the nervous systems of many other kinds of animals. Similarly well-integrated information has been compiled concerning general and comparative psychology. From the same point of view some of us have been trying to develop a general sociology, which even in its present imperfect state allows human social reactions to be viewed in part as the peculiar human development of social tendencies which also have their peculiar developments among insects,

birds, fish, mice, and monkeys; that is, among social animals generally.

Keeping this point of view, and with our background of studies of social organization, it is worth while to turn for a short consideration of the actual application of similarly objective studies in certain human groups. I pass over the possibilities of studying the peck-order in women's clubs, faculty groups, families or churches, to call your attention to some studies that have recently been published dealing with the social interactions of the Dionne quintuplets, since these will serve to throw light on a number of interesting points. (25)

In all questions of dominance in the group or of other forms of social inequality, we come immediately and continually upon the question of the extent to which these observed social differences are a matter of heredity and to what extent they follow differences in training or other environmental impacts. This is the old nature-nurture problem, other aspects of which have been discussed for years.

Driven by many different kinds of evidence, biologists have come to the conclusion that all men are not born equal. Applying this to social affairs we have the general assumption that many of the observed differences in social position are a result of the inherited differences depending on the vagaries

of bi-parental inheritance and more remotely on mutations of one kind or another.

Fortunately we have in the case of the Dionne quintuplets a natural experiment which deserves much attention. Detailed biological studies which appeared late in 1937 confirmed the general assumption that these much-discussed babies are an identical set of sisters. Biologically this means that all of them have come from one ovum which was fertilized by one spermatozoan. Soon after fertilization the early cleavage cells separated and produced five embryos, each with identical heredity. I shall not give the details of the evidence on which this conclusion is based. In addition to looking so much alike that only their regular attendants can tell them apart with any degree of sureness, there are similarities in finger and palm prints, in toe and sole prints, and in other anatomic details which point conclusively toward a common identical heredity.

A group of investigators from the University of Toronto have been studying the social reactions of the quintuplets and have reported observations from the twelfth to the thirty-sixth month of their age. At first the children were placed together in a play pen by pairs to observe their interactions; from the twenty-second to the thirty-sixth month they were observed as a group.

The available records do not allow an exact comparison with the peck-order I have described for various birds. The observers were interested in recording and analyzing the following bits of behavior:

1. Total contact reactions.

2. Reactions of one child toward another, which they call *to* reactions. A *to* reaction by one child will be a *from* reaction for the child receiving the attention.

3. Whether the reactions are initiated or are response bits of behavior. An illustration will help to make this clear. If A pushes Y, it is regarded as an initiated *to* reaction by A, while Y is credited with a *from* reaction. If Y pushes back, then this is a response *to* reaction for Y and a *from* reaction for A.

4. They also record which child watched which one.

I shall not use all these distinctions for my points can be made accurately with only part of them.

As shown in Figure 42, certain reactions are summarized in the top row for the entire period from the twenty-second to the thirty-sixth month, and in the lower row the same reactions for the last four months of the study, from the thirty-second to the thirty-sixth month. The left-hand diagrams give the total contact reactions during these respective periods. The center diagrams show the total *to* reac-

tions and those on the right give the initiated *to* reactions.

Let us examine the upper left figure. A had a

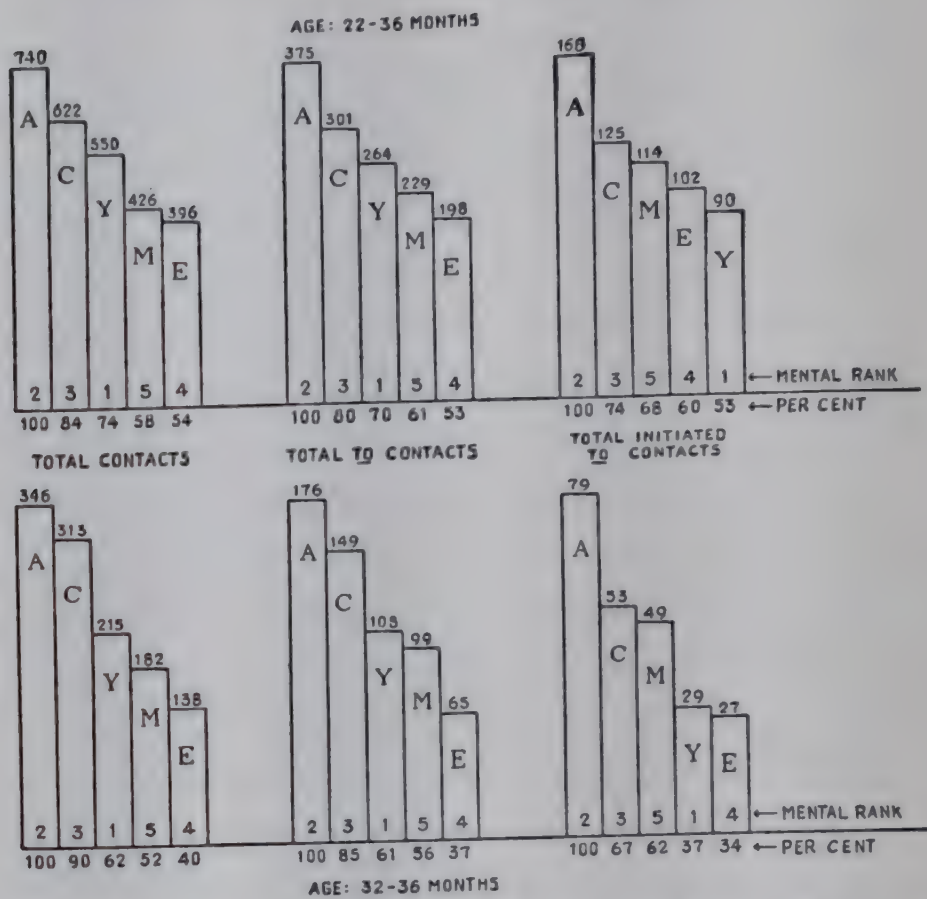


FIG. 42. The Dionne quintuplets also show evidence of a social organization among themselves.

total of 740 observed contacts directed to and received from her sisters. This is taken as 100 per cent. C had similarly 622 contacts, which were 84 per cent of A's, and so on, with Y third, M fourth, and E fifth. The order in total number of contacts then

is A, C, Y, M, E. This same order holds for total *to* contacts and for both total and *to* contacts in the thirty-two to thirty-six months' period. The diagrams on the right show that A initiated the most *to* contacts, and that C was next. Beyond that the order varies. For the whole period of observation (upper row) it is M, E, Y, and for the last period (lower row) it stands as M, Y, E.

The other available data do not always give this same order, but enough has been presented to show that, among these children identical in heredity and almost so in post-natal environment, there are social differences which can be recognized by the behavior of the children toward each other.

As the figures giving mental rank indicate, the correlation with intelligence is by no means perfect. Neither is the correlation with size. Y, the largest, and said in some ways to be the most mature of the five, ranks in the tests shown here from third to fifth. And while M, the smallest, ranks low, she is not the lowest, and other data show that in the percentage of her contacts which were self-initiated *to* reactions she ranks first of all these sisters.

These observed differences raise an interesting question: If heredity has been the same and the environment constant, how did the differences creep in? It is possible that there are unobserved, unrec-

ognized differences either in the handling of the children, in their early contacts with each other, or in their impacts with their physical environment which may have been cumulative enough to produce these social differences. It is also possible, as Professor H. H. Newman suggests, that the differences are environmental after all. We must remember that from the standpoint of A, C, Y, M, and E, their environmental relations began long before birth, and though the care given them since birth may have been practically identical in each case, it may not have been possible to erase environmental conditions impressed upon them during their seven critical months of intra-uterine life.

Whatever the reason, we have come to an interesting, and, I think, important conclusion, which is that animals with exactly the same heredity may still develop, even at an early age, graded social differences showing that one is not exactly equal to the other. We have indications that the same principle holds among birds, but even if present indications are finally borne out, the experiment will not be as elegant, in the strictly scientific sense, as are these observations on the Dionne quintuplets.

Finally, by way of review, there exists among flocks of birds, even though they may be identical to the human eye, a graded series of reactions within

the flock which allow observers to rank the birds in the order of their social dominance. This social order may be relatively hard and fast, as with hens, or more loosely organized on a give-and-take basis among pigeons and canaries. The factors underlying the social order in these birds are complicated and include such personal traits as age, pugnacity, sex in general and the reproductive cycle in particular, as well as such environmental factors as size of available space and the possibilities of establishing special territories. High position in the social order does not necessarily coincide with group leadership, although at times it does. The survival value of high position in the social hierarchy has not been demonstrated, but there are many reasons for suspecting that it may be felt in times of famine or during other periods of environmental stress.

The problems related to leadership, although mentioned, were not discussed exhaustively. Emphasis was laid on the importance to the leader of his followers, and on the existence of a pseudo-leadership in which the animal in front is taking direction from his apparent followers.

With the Dionne quintuplets it was demonstrated that social differences exist even with children that have identical heredity, and a theory of environmental differences was favored as an explanation.

In conclusion, the social organization observed in birds and other animals reminds one almost constantly of certain types of human social situations. The dominance-subordination relations of people are at times readily observed; at other times they are obscured by other social responses. When present in man, patterns of domination may be expressed in many more ways than in birds or mice. It may well be that the social hierarchies of chickens, canaries and men have much in common. Without taking the comparison too seriously, the fact that chickens, for example, have a relatively simple system of despotism may help explain, though it does not justify, the appearance of a similar social organization in man. Other types of social organization also exist among the other animals, and man need develop only that best suited to his unique situation.

VII. Some Human Implications

WHILE WE have been engaged in trying to assay the relative importance of the principle of co-operation among animals, we have given most of our time and attention to its manifestation among animals considered to be asocial or only partially social. In such animals it is an unconscious kind of mutualism, but its roots are deep and well established and its expression grows to be so spontaneous and normal that we are likely to overlook or forget it in the more striking exhibition of social co-operation among higher animals. Conscious co-operation is so comparatively new in an animal world many millions of years old, that we may underrate its strength and importance if we are not reminded of its foundations in simple physiology and primitive instinct.

When we attempt to apply to human behavior the same methods of analysis that we have used throughout toward other animal groups, we reach most interesting results when we select some phase of reactions of men in which integration has not developed

much beyond that found in some of the semi- or quasi-social animal aggregations which we have been considering in the lower animals.

Among the possible aspects of human behavior that meet this requirement and that lend themselves to biological analyses is the whole set of activities that center about the relations between nations. Even the most optimistic humanist will not maintain that these are at present, or ever have been, on as high a social plane as that which characterizes many of the personal interactions of mankind, or those of the smaller social groupings of men.

The most casual reading of recent events is convincing evidence that the modern international system is based on war. This final resort to violence has been regarded by many thoughtful people as inevitable, man being what he is, that is, the product by natural selection of the results produced by the struggle for existence; for the ordinary thoughtful person is not aware that the tendency toward a struggle for existence is balanced and opposed by the strong influence of the co-operative urge. Because of this common attitude toward war, and because of its fundamental importance to our species, I propose to cut through the shifting tangle of international policies down to the basic biological significance which it holds for us.

In doing so I must recognize these two fundamental principles, the struggle for existence and the necessity for co-operation, both of which, consciously or unconsciously, penetrate all nature; and I shall say now that we may find that these two principles are not always in direct opposition to each other; that there is evidence that these basic forces have acted together to shape the course of evolution, even the evolution of social relations among men and nations of men.

If, in the past, we have not had facts on which to base rational conclusions about national problems, it cannot be said that we have not had powerful emotions to drive us into one attitude or the other. It is very difficult to keep an objective, unemotional attitude toward the complex subject of the biology of war. We may not agree in our placing of the emphasis, but I trust that when we disagree it will be on a healthy intellectual level.

It is clear that we are entering a tricky field where, to a greater extent than usual, the evidence is not all in, and one in which much that we think we know is contradictory. No one can bring this problem into the laboratory for careful testing. We must do the best we can with information which is more incomplete and faulty than that on which we normally base our biological discussions. The human

importance of the subject justifies the risk. The present discussion will center about three main points:

1. To what extent do the underlying biological relationships tend to bring about war?

2. Is war biologically justified by the results produced?

3. Can the basic principles of struggle and of cooperation work together in the international relations of men?

Many men are aggressive animals. The similarities between human social hierarchies and those of chickens and other animals emphasize similarities of the drive toward dominance in the species concerned. Our immediate question is: Does this human aggressiveness mean that men have an inherent, instinctive drive toward war? The ideal way to attack this problem would be to rear sizable groups of people free from contact with outside influence or social tradition and see whether under these conditions they would instinctively engage in group combats in order to forward or defend group ambitions.

Such objective procedure is out of the question, but an interesting subjective inquiry has been made. In 1935, American psychologists took a poll among themselves on the question as to whether they believed that the tendency toward making war is an instinctive drive in man. Of those answering, well

over 90 per cent said that there is no proof that war is an innate behavior pattern. (129) Less than 10 per cent thought that war represents an instinctive reaction. I did not personally see this questionnaire but I am credibly informed that the question was stated fairly and did not suggest the type of answer expected.

This is a rather unexpected unanimity, and may be accounted for to a minor degree by the existence of one modern school of psychologists that doubt the possibility of instinctive action, particularly among men. I do not think they represent a large proportion of American psychologists but there may have been enough of them to have lifted the percentage high.

The opinion of the psychologists is supported by the independent judgment of one of the leading students of anthropology, Professor Malinowski, who said in his Harvard tercentennial lecture: (78) "All the wrangles as to the innate pacifism or aggressiveness of primitive man are based on the use of words without definition. To label all brawling, squabbling, dealing of black eye or broken jaw, *war,* as is frequently done, simply leads to confusion. War can be defined as the use of organized force between two politically independent units, in the pursuit of

tribal policy. War in this sense enters fairly late into the development of human societies."

It is not impossible to break down and re-make instinctive behavior, as the change in marriage customs since the days of the cave man shows us. Nevertheless, it is much easier to change learned behavior patterns, one of which these experts believe war to be.

We must still take account of individual aggressiveness, and the fact that man appears to be relatively easy to lead into mass combat. Even if war-making is not instinctive, if it is a learned pattern of social behavior, there is evidence that it has existed for some fifty centuries, and it would probably require at least a few centuries of intelligent and fairly concerted effort by those who do not believe in its utility to unlearn the habit.

There is a second important set of biological processes which at first sight appear to work inevitably toward the production of war. These center about the question of overpopulation, that is to say, about the relation human numbers bear to habitable land areas. This is the next primary problem which we must consider.

Over the world there is a limited range of habitable land; and thus far we have no intimation of any practical method of emigration to neighboring

and perhaps less occupied planets. And there is a rapidly expanding human population, which is even now becoming uncomfortably dense in the crowded nations. It is often said that this is a fundamental cause of tension which makes wars inevitable, as hard-pressed dense populations seek food in more amply-provided areas.

The desirable biological results of wars so induced have been, and still are, supposed to be two:

1. The dense populations are thinned to the bearable point as a result of the fighting, or

2. Superior nations, or races, are victors. They expand at the expense of the defeated inferior group and so occupy more of the limited space which is available for men.

Let us test these theories against the known facts. Roughly speaking, there are about fifty-two million square miles of land surface on the earth. (95) This includes the habitable plains of the temperate regions; it also includes the relatively uninhabited deserts, tropical jungles, and mountains. Approximately one-fourth of these fifty-two million square miles is desert or semi-desert and can support only a sparse population of men. This leaves roughly forty million square miles of non-arid land theoretically open to human habitation.

On this land there are living at present, accord-

ing to a 1935 revision of the estimated world population which was made by Professor Pearl, something over two thousand millions of people. This is almost exactly forty people per square mile of the whole earth's surface, or about fifty people per square mile, if the arid and semi-arid land is excluded. We can better visualize the meaning of these figures when we know that they are almost exactly the average population density for the United States; forty per square mile for the whole land area, and fifty per square mile if on land with fair rainfall.

A recent estimate of human population of three hundred years ago, tentatively advanced by Professor Pearl, is that in 1630 there were probably about 445 million people on the whole earth, or about eight per square mile of total land surface. (95) Dr. Pearl thinks that this was probably the largest human population which the earth had supported up to that time. Then came the opening of the Americas for settlement, and the beginnings of modern use of transport and manufacturing processes, and the scattering of information by modern methods. The result has been that in the last three centuries the population of the world has increased almost fivefold, from eight to forty per square mile, largely because food and shelter and mechanical energy were made available for five times as many people, and

because the development of modern science made the world safer for them.

In these three hundred years the world population has doubled, on the average, approximately every sixty-four years. Today mankind is increasing in numbers at such a rate that *if the increase should continue* as it was going in 1935 we could expect another doubling of the number of people in the world in approximately seventy years, and we should have about eighty people per square mile in the year 2005.

What then? Will not the coming generations at some time be obliged to fight for their place in the sun?

This prospect is somewhat altered, however, by the fact that many students of population trends believe that the rate of human increase is slowing down. In the case of the United States, Dr. Baker, (20) economist of our Department of Agriculture, has estimated recently that unless present trends are changed (and they may be) there will be a further population increase in the United States of only about eight million in the next two decades. He thinks that the population will then have reached its maximum, *if conditions remain as they are today.* Thus, according to Dr. Baker, we are looking forward to a maximum population of less than 150

million people, or less than fifty for every square mile of our country. Others put the figure higher, but I know of no expert who expects our American population to double itself again unless there is a radical increase in available energy or in other aspects of our living conditions.

For the world as a whole, Dr. Pearl estimated in 1936 that, *if present trends continue,* as they may not, the world population will reach a maximum of about 2,650 millions by the year 2100. (95) This is a density of about fifty persons per square mile of land surface on the globe, counting good and bad land alike.

I must dissociate myself from any responsibility for these and similar estimates. I fully realize, as do their authors, the pitfalls inherent in such predictions. Human trends being what they are and have been in the last three hundred years, this is as good an approximation as can be made at present, and with all its faults it is worth considering.

The important aspect to me is that we do not have reason to expect in the United States or in the world a continuation of the unprecedented rate of increase of the last three centuries, or even a continuation of the present rate of increase. Unless population experts are all at fault, the rate of re-

production among human animals is slowing down, just as the rate of increase in non-human populations slows down as laboratory containers approach an overcrowded condition. In fact, few animal populations approach the limits of their food supply in nature.

The reasons for this are not clear, though they appear to be connected with the ease of securing available energy, food and shelter. As men approach the bearable limits of these necessities of life there occurs an increase in birth control. This is shown in Italy, where, according to figures given in *The Statesman's Year Book,* (114) despite continued propaganda for a higher birth rate the actual number of births fell over 12 per cent from 1922 to 1936 (Figure 43). Thanks to a similar decline in death rate the significant percentage of births which are canceled by deaths has remained fairly steady. In England, where there has been no great effort to encourage population increase, the deaths in 1922 were 62 per cent of the births; in 1935 they were 81 per cent. Perhaps the success of Italian efforts is to be measured by this comparison with England rather than by the fact that under propagandist pressure their birth rate has actually decreased. In Germany, the present regime has not been in power long enough to establish a trend. The graph (Fig-

ure 43) shows that beginning in 1934 there has been a dramatic decrease in the percentage of births canceled by deaths; actually there has been a decided increase in births. Recent analyses in the *American*

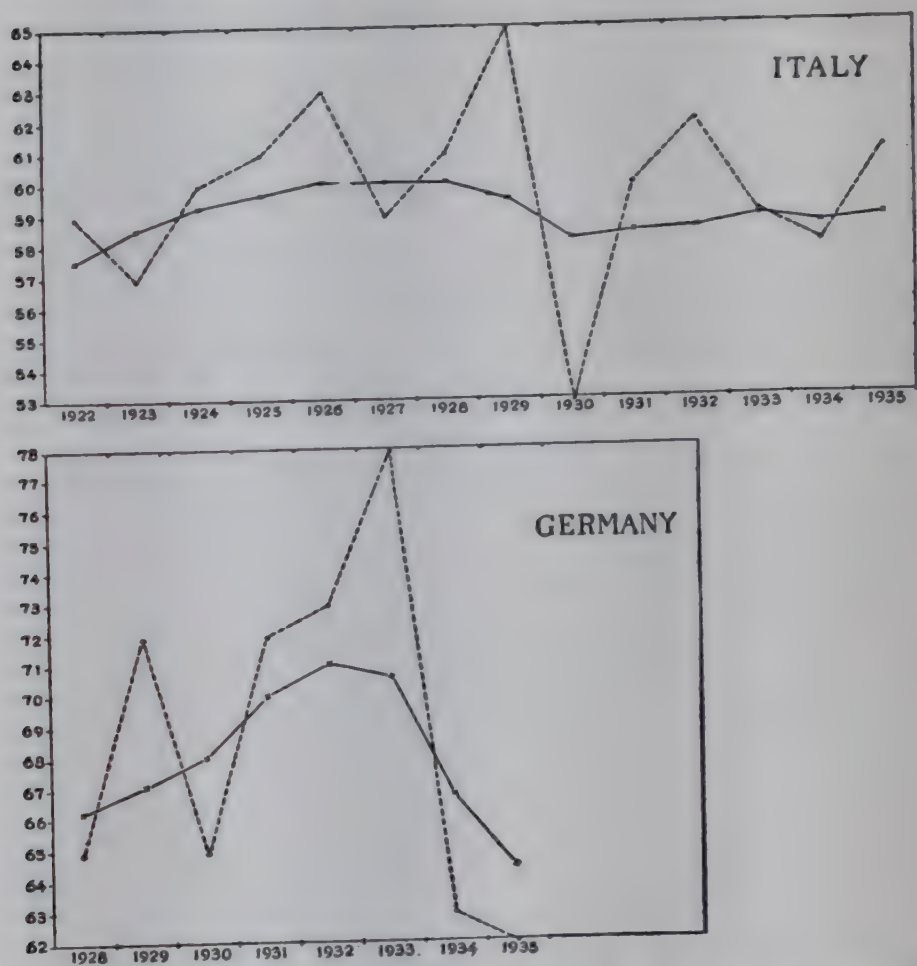


FIG. 43. The percentage of births that were canceled by deaths for the given years in Italy and Germany. The higher the trend line, the slower the population is growing and vice versa. The broken line connects the observed points; the solid line shows the mathematically smoothed trend line. (Data from *The Statesman's Year Book.*)

Journal of Sociology indicate that the present opinion is that the increase in the birth rate may be the result of a campaign against abortion which in pre-Nazi times terminated over one-third of the pregnancies. (58, 125) One can deduce from general biological experience, despite the current German data, that the population almost automatically adjusts numbers within its physical and biological limitations. Doubtless eventually this mysterious process of population adjustment will be analyzed. At present we have made some progress toward an understanding of the factors involved in non-human populations, but have little objective knowledge to report where men are concerned.

It is of course possible to increase the present food supply of the world enormously. It has been estimated that if our present biological knowledge were consistently applied we could raise food enough to supply at least ten times the present world population, instead of the 25 per cent increase to which we are looking forward by the year 2100. Presumably by that time we shall have learned much more than we now know about intensive methods of food production.

Let us take one simple instance only. In the United States we are substituting gasoline-driven farm machinery for horse power in agricultural work.

The land required to produce feed for one horse will equally well provide food for a man. Baker, the agricultural economist cited earlier, estimates that the land released annually by this change in farm technique can be turned to growing human food almost as fast as our population is increasing.

The question seems rather one of adequate food distribution than of shortage of food. Under conditions which we can visualize at present there seems little likelihood of a real food shortage for the world as a whole.

If, however, these conclusions prove to be completely wrong, and the world population is now or will become too high by biological standards, there is still the question as to whether war is a sound and sufficient means of controlling population growth. The theory that war is an efficient means of stopping the increase of mankind is so contrary to fact that I allow myself to say No in the first place and present the evidence later.

The immediate effect of a war upon the civilian population is to depress the birth rate and raise the death rate on both sides of the line, whether in the winning or the losing nation. Figure 44, taken from a study by Pearl on population trends during the World War, gives these data for the unoccupied parts

of France, for Bavaria and for England, from 1913 to 1918. (92)

In 1913 deaths and births in these parts of France were almost equal; in 1918 there were approximately

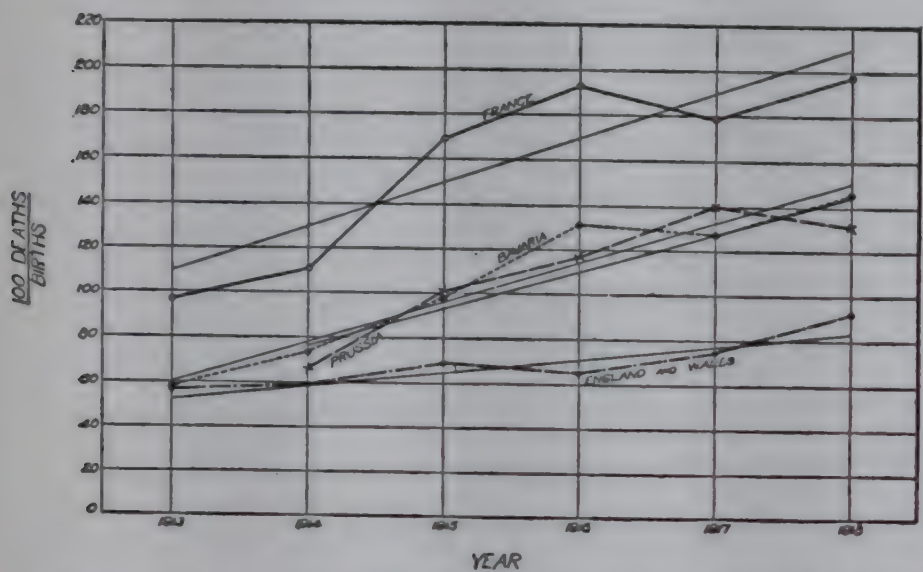


FIG. 44. The percentage which deaths were of births steadily increased during the war years in France (non-invaded departments), Prussia, Bavaria, England and Wales. (From Pearl.)

two deaths for each birth. In Bavaria, in 1913, there were five births for every three deaths; in 1918 there were three births for every four deaths. The trend lines in Figure 44 for these two countries run almost parallel, though France was invaded and losing in much of the fighting while Bavaria was free from foreign troops and part of a winning nation until near the end. As usual, analysis of such a situation is not simple. Bavaria, although enjoying the

psychological advantage of belonging apparently to the winning side, suffered the physiological disadvantage of an increasingly severe food shortage, while France averaged an adequate food ration. In England during the same time, where there was neither invasion nor starvation, there was the same tendency toward increase of deaths in proportion to births, though less marked. These statistics, of course, do not take into account the almost unprecedented death rates in the fighting lines.

Temporarily the population growth was checked, but almost immediately following the close of the war the ratio of births to deaths resumed their prewar trend lines. Pearl, writing in 1921, (93) summed up his study in these words: "Those persons who see in war and pestilence any absolute solution of the world problem of population . . . are optimists indeed. As a matter of fact, all history tells us, and recent history fairly shouts in its emphasis, that such events make the merest ephemeral flicker in the steady onward march of population growth."

Fifteen years later, in 1936, (94) Pearl again wrote, alluding particularly to the effects of wars of conquest by one nation to acquire the territory of another: "The world problem of population and area, however, remains unaltered in theory, though practically it will have been made worse because of the

extravagantly wasteful destruction of real wealth that war always causes. This is the problem that is really serious—how can forty persons be maintained for every square mile of land surface of the globe—good, bad and indifferent land together? War cannot enlarge the land surface that must support mankind; it has never diminished the total number of people who want to live on it except by a tiny fraction for quite a brief period. There is no way out of the dilemma by the pathway of war."

It is a comparatively new idea that population can be controlled at all except by famine, pestilence, and war, which have been regarded as acts of God. Acts of God or not, we can no longer tolerate famine or pestilence if we have the power to prevent them; and lacking such power we intend to get it as soon as it is humanly possible. Among dispassionate, expert students, war has similarly lost caste as a means of population control, though the man in the street has not yet learned this.

Instead of the dubious check these agencies furnished there is a steady turning to birth control, even in the countries where it is most surprising to find this. In Germany and Italy, although artificial stimuli are being applied to keep up the birth rate, some kind of birth control evidently is occurring.

There is significance not only in the average

density of people per square mile of the earth's surface, but also in the population density of the most crowded nations. The degree of crowding in certain countries with whose problems we are familiar is shown in the following list. The figures given are slightly rounded statements of the average population density per square mile of land territory. The most densely populated countries of the world are listed here in order (94):

COUNTRY	PEOPLE PER SQUARE MILE
1. Belgium	700
2. England and Wales	680
3. Netherlands	660
4. Japan	450
5. Germany	360
6. Italy	360
7. China (proper)	300
8. Czechoslovakia	270

For many purposes it is hardly fair to compare the relatively small countries like Belgium and the Netherlands with others like Japan or Italy which are larger but contain a high percentage of waste land. For our purposes, however, the list as it stands is fair enough; such data represent the facts we have to face.

At present about two and a half acres are required

to supply food to one person, if the soil is fair to good and the husbandry is good according to present standards. This means that under modern conditions of agriculture the upper limit of a relatively self-contained population is about 250 people per square mile. It will be seen that Belgium with its 700 per square mile almost triples this upper limit, and that England and Wales and the Netherlands more than double it. Such high population densities can be supported by trade conducted with other countries on a large scale. They could also, as we have seen earlier, be supported by improved methods of agriculture. An Italian expert on populations said in my hearing some years ago that population pressure is not a direct cause for war, but can be used by a clever leader to range a nation behind aggressive policies which lead to war. In the short run that is easier than to educate people to apply the available knowledge which would allow Italy, for example, to feed her present population, and more, from the products of her own soil.

It is time now to turn to the second of the questions concerning the biological background of war. In the light of the preceding discussion we can restate this question as follows: Although underlying biological relationships do not necessarily lead to

war, is not war biologically justified by the results produced?

If war does benefit the race in distinct and unique ways, then the biologist must favor a system of society which will bring about the proper kind and the correct number of wars to produce the best racial selection. If war, on the other hand, tends toward human deterioration then the biologist must oppose a system of international relations based on war. Again it is a question of evidence.

The matter of *individual* biological selection is one that is fairly obvious even to the layman; and his conclusion that the direct results of war are harmful biologically has been well supported by scientists whose interest in the subject is more inclusive than their natural sympathy for the young men of their acquaintance who have incurred wounds or have been gassed or have suffered severely from some of the typical wartime epidemic diseases. The work of David Starr Jordan before 1914 is classic; (70, 71, 73) but the evidence furnished by the World War is more important to us. American experience at that time is best set forth in the slender book by Professor Harrison Hunt (67) of Michigan State College, who studied the records of the American army, using modern statistical methods.

He was left with no doubt that war selects the

best of our young men for exposure to wartime hazards. We have space for one bit of evidence. Hunt found that for the drafted American army, 83 per cent of the mentally defective were rejected; those of normal mentality and the 17 per cent who were only slightly subnormal were held for service. A good geneticist would have reversed the procedure, sending the mentally deficient out into wartime risks and keeping the others at home to continue the race. But this is so contrary to fact in all the standards by which armies are selected that it seems faintly ridiculous in the telling. Personal selection, so far as it exists in modern warfare, selects the individual to be killed or wounded because he is physically or mentally superior to those who are left at home. (64)

The ill effects of this selection among the young men are evident in a nation where war losses have been heavy, but they are less drastic for people as a whole than they might be if it were not for various mitigating factors. To date only half the race has suffered in so-called civilized warfare, since women have been exempt from actual combat. Also many young men return who, though wounded and perhaps otherwise handicapped, are still physically capable of passing on their germ plasm to succeeding generations. And even in populations badly shattered by war most of these genetic ill effects could be ob-

viated if monogamy were less of an ingrained human practice.

The effects of severe wartime epidemics, which are usually the cause of more deaths than the actual fighting, are subject to the same comments; but with these epidemics the civilian population is also directly affected, as was the case with the influenza pandemic that swept the world in 1918, and carried off in a day more civilians than did many spectacular air raids combined.

General epidemics tend to fall most heavily on the old and the young; biologically we are most interested in the fate of children and young people. Disease and undernourishment drastically reduced the younger population in places well away from the fighting lines in the last war. Homer Folks, (47) U. S. Red Cross commissioner, testifies that in some sections of Italy 60 per cent of the children failed to survive wartime conditions. The children of Germany and of Poland suffered greatly.

If he could know that such severe exposure eliminated the relatively weaker specimens and left a stronger, hardier race, the biologist could reconcile himself to the death of these children, though emotionally he might rebel.

But this rationalization is impossible. Study of the after-effects of epidemics upon children (45) does

not show a group of sturdy survivors, with all the weaklings eliminated. Rather, the later history of these children shows that they have a lower resistance to the next severe disease that strikes them. Apparently many such children, though surviving, are weakened for some years thereafter.

Similarly, the children back of the battle lines include many whose experience left a mark, and who recover only slowly from its injurious effects. They were not a selected lot, and their own generation has suffered. Fortunately all our evidence indicates that those who survived are able to pass on their inherited qualities unimpaired to their children; but many are unable to provide for their families the physical care and conditions for living which make for the fullest development of inherited potentialities.

Perhaps a sane and cautious quotation from Professor Holmes of California will be a fitting summary for this section. In 1921, Holmes wrote: (63) "On the whole it is quite probable, I believe, that the effect of military selection is harmful. . . . It is a matter of serious doubt whether the beneficial factors come near outweighing the adverse selection of battles."

What are some of the beneficial effects which this statement suggests may exist? One of them is that

war is necessary to maintain racial vigor. This is a matter on which statistics are not available, and on which personal opinion must play as reasonable a part as it can.

To me it seems a misreading of history that leads to the justification of war as a means of keeping up the vigor of the race. I should say, rather, that wars have frequently revealed the loss of racial or national vigor among a people made soft by easy living, which in turn had been made possible, at least at times, by a long series of successful wars of conquest.

Anyone who attempts to maintain the thesis that wars do keep racial stocks vigorous—and there are biologists who believe this—is troubled by the Chinese people. This much-discussed and frequently invaded land was populated by the forerunners of the present Chinese during the days when Egypt, Assyria, Babylon, Greece and Persia, to name no more, were fighting the wars recorded in our general histories. Those warlike peoples have lost their racial vigor but the Chinese, who have been relatively peaceful, have retained it. This stumbling block cannot be removed by denying racial vigor to the Chinese; they have, in the past, absorbed too many temporary conquerors, and have occupied and are occupying by peaceful penetration too much of the earth's territory, to be dismissed as a racially decadent people.

There are anthropologists who reckon them biologically the most advanced people living today.

There is another allied but somewhat different theory regarding the human benefits conferred by war which holds that even though in direct personal selection the war system is dysgenic, it does tend to select the fittest races and nations for survival. This theory is usually applied to European history, where in the long struggle of advanced European nations against backward poorly-equipped natives of America, Asia, Australia and Africa, victory has eventually rested with the Europeans. Whatever the intrinsic human merits of the case, a question on which Hindus may disagree with Englishmen, there can be no doubt that such conflicts have been won by the nation which possesses the more modern social organization and the better gadgets with which to fight; and the winning nation has not hesitated to levy on the weaker one for whatever of its possessions and services it could utilize for its own advantage.

When, however, one European nation fights another, as, for example, France and Germany, who can maintain that the nation that won at Waterloo and in 1918 is superior to the people who won at Leipzig and Sedan? Or, to come closer home, does the fact that the Confederacy lost the war between

the States prove that the white people of the South are racially inferior to those of the North?

Actually, of course, we are not fighting racial wars at present. What race won the World War, or for that matter, lost it? Modern warfare among so-called civilized powers probably does result in victory for superior wealth, better organization, shrewder propaganda, and other social achievements, but we have little good evidence to link these social attributes with racial stock, in spite of contemporary German determination to assume the connection.

Let us allow Popenoe and Johnson, (99) recognized students of eugenics, to summarize this whole inquiry into the biological justification of war. Writing in 1918, when the subject was near the top of men's minds, they said: "When the quality of the combatants is so high compared with the rest of the world as during the Great War, no conceivable gains can offset the loss. It is probably well within the facts to assume that the period of the late war represents a decline in inherent human quality greater than in any similar length of time in the previous history of the world."

It seems to me that such evidence and reasoning as I have presented indicates pretty clearly that the present system of international relations is biologically unsound. Attempts which have been made in

the past to lend biological respectability to the present system by regarding it as an expression of an inevitable struggle for existence have overlooked not only its defects as a selecting agent but, more serious, have often not even been conscious of the existence of another fundamental biological principle, that of co-operation. Is it possible to envisage a system of international relations which will be fairly based on both these aspects of biology?

One of the first questions to be examined is that of the size of the co-operating unit practicable in such a system. It is possible to make a case for the present human social divisions, where nations of various size co-operate within their own boundaries though competing with each other for various types of supremacy. Within each of these nations are graded series of groupings in great variety, which also co-operate within and compete across their tangible or intangible boundaries. Here immediately we come across an important qualitative difference in the competition. Within each nation this intergroup struggle is normally carried on by approximately peaceful and orderly means. By contrast it is accepted that the competition across national limits, usually peaceful and orderly, may at any time break down into the socially backward phenomenon called war; and even in periods of peace and social

progress much of the average nation's energy, wealth and forethought is diverted to preparing for the next war.

Peaceful intergroup competition within a nation has come to rest, in the first place, on habit, preference and a realization that only temporarily is an advantage gained by violence; and, in the second place, on a government, often set up by mutual consent of the competing groups, which is strong enough to block or stop cruder appeals to force, and which is expected by them to do so.

The suggestion has been urgently repeated since the time of Sully, (61) the great minister of Henry of Navarre and France, that there should be a similar international organization. Theoretically there is almost everything to be said for this proposal. Such an international organization might be set up much as the federal government of our country was planned, to supervise the functioning of the different states. This system calls for representative government, a relatively unbiased court of final judicial appeal, and certain potential police power, which in our American experience has been used but rarely on a national scale.

The present League of Nations, even in its most hopeful days, did not show more than remote possibilities of equaling on a world scale what the British

Empire has done fairly adequately of recent years for more than one-fourth of the earth's land area. Any future international body which will undertake to apply the balanced principles of struggle and co-operation on a global basis must, among its other qualifications, avoid certain outstanding mistakes of the present League.

It cannot be really co-operative if it is basically a league of victor nations formed to administer a punitive peace treaty, for this is hardly a step in advance of the time-honored national alliances for defense and offense, which are co-operative only to be destructive. It must not be dominated in any department by the representatives of any one nation, not even when that nation is as intelligently, and shall I say selfishly, benevolent as England and its dominions today. It must be so organized as to secure and hold adherence from the great majority of nations. As a step toward this end, the biologist's international system must be a dynamic organization capable of and designed to effect changes rather than set up to preserve any given status quo, regardless how favorable for the predominant powers.

Biology teaches the inevitability of change, if it teaches anything. We must have some device in our system which will allow for needed changes, some means of making those compromises at which the

English and the French are so proficient in their internal affairs. In international as in legal circles, we must have some peaceful means of declaring a defunct nation to be in fact bankrupt or unable to manage its own business, and to distribute its assets among the proper creditors.

When such a system is installed there will need to be not only the means for international consultation, and a hearing for the troubles of the world; there will also be the necessity for courts of international justice. One of these may well grow out of the present World Court at Geneva, patterned on the Supreme Court of this country; another might be a development of the international court of arbitration which has been located for many years at The Hague.

At this point we come to a serious divergence of opinion. Should these courts be supported by police power? As a realistic biologist it seems to me that international police force will probably be a necessity in those cases when a nation or a section of a nation attempts to raise itself in the peck-order of governments by direct action rather than waiting for the results of the more just but slower pressure of world opinion. Much of the police activities should be limited to such duties as are now exercised by our federal marshals, but in my judgment there would

need to be the possibility of the use of even stronger police pressure.

But it is certain that if an international organization is to succeed, police power must be used very rarely. The attempts of the British government to coerce the American colonies or the Irish people are conspicuous as a demonstration of the frequent failure of massed force to compose complex human maladjustments. It is noteworthy that such enforcement has not been used in the long and successful operation of our own Supreme Court.

Practically, it is possible that nations will join in an international enterprise which is limited to consultation and judicial review of all disputes long before they will relinquish any other phase of their jealously guarded sovereignty to such an international organization. We may even be able to work out a method of international co-operation based entirely on patience, wisdom and justice, though in the light of past experience this seems at present unlikely.

Such a world organization will never be perfect. Man is not. Neither is the government of Chicago, of Illinois, of our United States. And yet who would not prefer to live in Chicago, even back in the gangster era of the nineteen-twenties, rather than in the period of greater individual freedom for privileged

people that London or Paris of the Middle Ages afforded?

A thoughtful and sincere biologist may object that the world is too large an area for a successful co-operative unit; that we need units intermediate in size to allow for human evolution those advantages which Professor Wright has demonstrated for populations intermediate in size. To such objection one must reply that, as to the latter point, the maintenance of smaller co-operative and competing units within the larger one is part of the scheme as sketched. And to the first, that of the great size of the earth, it needs only to be mentioned that thanks to recent improvements in transportation facilities, New York is in point of time as near the Orient as it was to Los Angeles in 1885; and there are few places on the globe as remote from Washington as was San Francisco before the Union Pacific Railway was built. In transportation and communication, and in community of essential human interests, the world is ripe for a workable international organization.

From the standpoint of pure biology, disregarding considerations that may seem to smack of the social sciences, the mortal enemies of man are not his fellows of another continent or race; they are the aspects of the physical world which limit or challenge his control, the disease germs that attack him and his

domesticated plants and animals, and the insects that carry many of these germs as well as working notable direct injury. To the biologist this is not even the age of man, however great his superiority in size and intelligence; it is literally the age of insects.(7)

This is a fact which must have repeated emphasis. In the tropics there is only the narrow strip along the Panama Canal and similar small areas in which man has shown the ability to compete successfully with the insects; and the techniques of this competition are too expensive as yet to apply along the vast rich stretches of the Orinoco River, the Amazon or Congo; there, undoubtedly, the insects are in control. In countries like India and Russia mosquito-borne malaria is a plague which saps the energy of those enormous populations as it does today in our own South.

There are good biological precedents for such competition between different types of organisms as that between man and insects or between man and bacteria. In fact, with almost negligible exceptions, the only kind of mass slaughter for which there is precedent in animal biology is found in interspecific struggles. One species of animal may destroy another and individuals may kill other individuals, but *group* struggles to the death between numbers of the same

species, such as occur in human warfare, can hardly be found among non-human animals.

These techniques by which we can successfully combat our enemies, the insects, and the viruses they transport are too expensive for the world today. They are too expensive because even the peaceful nations are using so much of their resources for buying and building armament on an unprecedented scale, apparently to make one more experimental test of the fact that war is biologically indefensible.

In our struggles with our physical environment, with disease germs and insects, we have ample opportunity for the struggle for existence, and stimulus enough to apply to the limit the principle of co-operation.

Unconsciously or consciously, the innate urge toward co-operation appears even under circumstances where it would seem least likely to be fostered.

Even in the most seriously war-torn countries, as in Spain today, when one is withdrawn from the actual scene of battle one finds the common people engaged as best they can in their normal activities of providing food, clothing and shelter for themselves and their families, with the ineradicable drive toward constructive co-operation that we have found evident throughout the animal kingdom. Such co-operative activity will reach through a family, from

family to family, from city to city and even across frontiers.

These normal activities can be wiped out in a few minutes by the exaggerated expression of the struggle for existence which we call war, extended beyond all biological justification and become, as Malinowski has said, "nothing but an unmitigated disease of civilization." (78)

It is a disease of long standing which even under most favorable conditions we must not expect to see cured overnight; but the outlook is not without hope. There seems to be no inherent biological reason why man cannot learn to extend the principle of co-operation as fully through the field of international relations as he has already done in his more personal affairs. In addition to the unconscious evolutionary forces that play on man as well as on other animals, he has to some extent the opportunity of consciously directing his own social evolution. Unlike ants or chickens or fishes, man is not bound over to form castes or peck-orders or schools, or to wait for a reshuffling of hereditary genes before he can discontinue behavior which tends toward the destruction of his species.

VIII. Social Transitions

WHEN DOES an animal group become truly social? This question has already arisen in preceding chapters and is difficult for a thoughtful biologist to answer with confidence.

One school, now happily small, regards society as beginning when animals first display a social instinct. (16) By this they probably mean that social animals have inherited a behavior pattern that causes them to live together with others of their kind in more or less closely co-operative units. Others consider that animals are social when they carry on group life in which there is clear evidence of a division of labor. (42) There is also the frequent suggestion that only those animals are truly social whose behavior is an extension, directly or indirectly, of familial behavior. (119)

For myself, I regard those groups in which animals confer distinct survival values upon each other as being at least partially social; this is the conception that has most often appeared in these pages. (3)

And from a still different point of view, those who would stretch the idea of social living rather widely would say, as I have indicated in Chapter V, that when animals behave differently in the presence of others than they would if alone, they are to that extent social. (115)

These ideas concerning what constitutes a proper definition of animal societies, while not necessarily mutually exclusive, are sufficiently different to raise difficulties when one tries to examine critically the useful general concept of social life; it will be profitable to study some of them separately.

As to the first definition, that social life must be limited to those animals that possess a social instinct, an inherited behavior pattern, it is hard to demonstrate beyond reasonable doubt that many patterns of social behavior are in fact inherited. Is the tendency of many fishes to form closely-knit schools inherited or an early-conditioned bit of behavior? There is some evidence that it is inherited, but we are not yet sure of it. But if it were granted that such schooling tendencies are innate, it would not necessarily follow that they are instinctive. There are different degrees of complication of inherited behavior patterns, from the relatively simple reflex action of an unborn embryo to the complex mating behavior shown, for example, by some insects and

by rats. The exact determination of the place in this line of increasing complexity at which an action ceases to be a simple reflex and becomes a more elaborate tropism, or the point at which the tropism gives way to an instinct, has never been made. That is, we do not know just how far down in developing patterns instinctive behavior extends.

There is the added complication that the word "instinct" has been loosely used. The most workable definition that I have arrived at is a modification of an older one of Wheeler's: An instinct is a complicated reaction which an animal gives when it reacts as a whole and as a representative of a species rather than as an individual, which is not improved by experience, and which has an end or purpose of which the animal cannot be aware. Too frequently the word has been applied to any bit of behavior whose origin and motivation the observer did not understand, with the unfortunate paradoxical implications that thereby the action was explained and at the same time could not be further explained. As a result of this uncritical usage many careful workers disapprove employing the word under any conditions, and particularly in the field of social activities.

In recent years some students of social life have attempted to avoid the term "social instinct," while

employing the same fundamental idea under the thin disguise of "social appetite," (122) "social drive," or "group interattraction," (100) which is apparently understood as inherited. These contributions to a more picturesque language do not necessarily advance our understanding of social behavior.

Still others sincerely believe that behavior patterns are not inherited, which seems to me a clearly untenable position. But however strong my belief in the actual inheritance of social behavior I do not consider it helpful to make the possession of such an inheritance the major criterion of social living; it is not a practical working test as to what constitutes social life.

If division of labor be used as a touchstone the same type of difficulty arises. We do not know how to determine when such a division becomes sufficiently general to merit being called a social attribute in the stricter sense in which we are now using the term. For example, there is a division of labor which is associated with sex and which is almost as extensive as sex itself. When does this particular division of labor cease to be merely an expression of sex and become social in the commonly accepted use of the word?

The mention of sex brings up again another important definition of social life among animals which

has already been listed. This states that only those groups which have grown out of the persistence of sexual and more especially partial or completely familial relations are truly social. This point of view has been touched upon with some sympathy in the first chapter. There is an important relationship which underlies this definition; many highly organized social groups do develop from the continuation and extension of family ties. But though this condition has given rise to many of the better developed social units, care must be taken not to regard its presence as the essential difference between the social and the sub-social. As Professor Child (32) has suggested, boys' gangs, girls' cliques, and men's and women's clubs present difficulties to one who wishes to define all societies as extensions of familial relationships. It is quite possible to regard such social phenomena as expressions of other aspects of the social urge which have developed independently of paternal or fraternal interactions. There are counterparts of these human groups among other animals, as well as counterparts of the extensions of family life. The overnight aggregations of male robins, the long-continuing stag parties of male deer outside the short rutting season, (38) the flocks of mixed species of birds common in tropical regions (Beebe tells of one made up of twenty-eight individuals represent-

ing twenty-three species, (24)) schools of fishes, and the swarms of animals spoken of in the second chapter, all of these instances test and stretch in varied ways the idea that only those continuing aggregations of animals which grow out of sexual and familial interrelations are truly social.

Inherited behavior patterns, the forerunners of instincts, and sexual differences extend down to the protozoa; so do continuing family groups, especially in the form of structurally connected colonial organisms. Group survival values are present in groups of organisms in which sex has not yet evolved, as well as among those in which sex is elaborately developed. In the light of such considerations it becomes exceedingly difficult to establish any one line above which life is to be regarded as truly social and below which we have only differing degrees of sub-social relations. Here, as happens so frequently in biology, we are confronted with a gradual development of real differences without being able to put a finger with surety on any one clearly defined break in the continuity. The slow accumulation of more and more social tendencies leads finally by small steps to something that is apparently different. If we disregard the intermediate stages the difference may appear pronounced, but if we focus on these intermediates it will be only for the sake of

convenience that we interrupt the connecting chain of events at some comparatively conspicuous link and arbitrarily make this the dividing point, when one is needed, between the more and the less social. It must be recognized that any such division is a matter of convenience rather than a natural break in the development from mass or simple group behavior to highly evolved social life.

For our purpose in the present account it is sufficient to recognize that the well-integrated social systems of man and other mammals, of bird flocks and of insect colonies, exhibit among them the highest expressions of social abilities that have evolved. In the range of social development shown in these animals we find attributes that are truly social in the most exclusive use of the word. But these highest expressions of social living have their roots in tendencies that in the form of unconscious co-operation accompany animal aggregations extending throughout the whole animal world, as well as to some extent among plants. Conceding then the difficulties in the way of making any exact definition of social behavior, I wish to present some of the social implications of mass physiology, particularly among well-integrated societies of animals.

One of the characteristics of social life among the insects is the presence of castes (121) which perform

different functions within the colony. With many social insects the division of labor has developed to such an extent that the animals which do different work have bodies that are more or less structurally appropriate to their principal tasks. The reproductive female has a greatly enlarged abdomen; the soldier grows up to possess large jaws and heavy armor or other protective and attacking devices; a worker may be large or small or medium in size, according as its size will best suit for some of the varied tasks necessary for the life of the whole colony. The situation is greatly different from that among human social castes, where a member of the aristocracy may be as husky of body and as empty of mind as the most menial of the working caste.

The only physically distinct castes to be found in man and the higher vertebrates are those associated with sex. In sexual forms there is always a division of labor with regard to the primary sexual functions except in those rare cases, usually low in the evolutionary scale, which at one and the same time are both male and female. With many, aside from producing eggs rather than sperm, it is difficult to find a division of labor or of appearance between the sexes. With others, particularly among the more specialized animals, there are differences in sexual behavior and responsibilities which are associated

with the more fundamental distinctions of sex. Frequently, as in man, these differences have developed into fairly distinct behavior patterns for the two sexes, until each sex is practically a distinct caste, almost in the sense used in discussing castes among the social insects.

Sex is usually determined by differences in heredity which are associated with the combination of chromosomes (37) and of the bearers of heredity (genes) that are found in the sperm and egg whose union gives rise to the new individual. Such determinations occur at the time of fertilization and sex is normally unaltered thereafter.

Exceptions occur which demonstrate that for certain animals this normal means of sex determination can be overruled by environmental differences. Many of these cases are interesting and significant but their full consideration here would draw us off the main thread of our present discussion. We shall follow only those instances in which changes in sex are associated with the near-by presence of other individuals, considering here two widely differing cases which have been carefully investigated in recent years.

Professor Coe (35) of Yale has spent much of his time studying the sex ratios and sexual changes in oysters, clams, marine snails and other related forms.

In many of these mollusks he has found that the sex ratios vary greatly in different environments, and has reached the conclusion that frequently among these animals the expression of an innate sexual tendency may be in part suppressed or stimulated, as the case may be, by the environment in which any given animal is living.

A pertinent case is that of a set of marine snails of the genus *Crepidula*. Three of these "boat-shell" snails are common animals in the coastal waters of southern New England. Their sexual history follows similar outlines. After a juvenile period which is essentially asexual, the growing *Crepidula* becomes first a male and then later, sometimes only at long last, it transforms into a female. A typical species to follow through this transformation is *Crepidula fornicata*.

When young, these animals move about, but as they become older and larger they settle down in one place on a wharf piling or a rock or another shell. If the larger, older animals are broken loose the soft parts are usually destroyed by some predator before they can reattach themselves, leaving behind the relatively heavy shell. Frequently they form large chains of individuals, of which a simple example is shown in Figure 45. The large, bottom snail

is dead. Attached to its shell is a large female which in summer actively produces eggs. Above her are two individuals that are undergoing transformation from male to female. Scattered about over these are

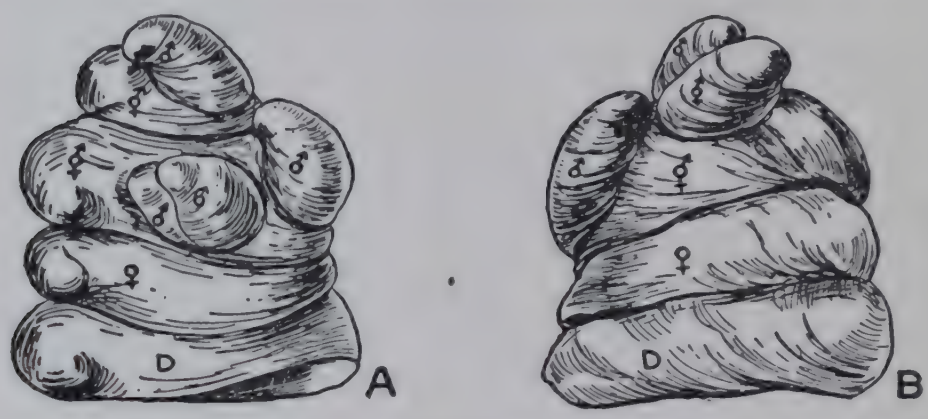


FIG. 45. *Crepidula fornicata.* (A) A basal female is attached to a dead shell (D); two individuals are in transition stages and there is one male at the apex; three motile supplementary males are in mating position on the lower transition individual. (B) same group from the left side. (From Coe.)

four smaller snails which are still functional males and which can and do move about. Each male has a long slender penis by means of which he transfers sperm from his body to an appropriate receptacle in the body of the female. Several males may participate in the insemination of a single female.

The growth of these snails is fairly rapid. A young snail hatched out early in the summer may, before autumn, become a functional male about 16 mm. long, which is about two-fifths the size of a fully

adult female; during the following year he will probably transform into a female.

The relationships which Dr. Coe observed at Woods Hole may be summarized briefly. Some two hundred young males were taken from their normal surroundings and placed in separate containers in the laboratory. Two months later only 11 per cent were still functional males; 15 per cent had transformed completely into functional females and the other 74 per cent were on their way in that direction. Random collections of snails of similar sizes which had been left alone in their natural associations showed that 85 per cent were still functional males and only 3 per cent had fully changed into females.

Coe summarizes his work with this and the other Crepidulas as follows: "There is no doubt but that in each of these three species of *Crepidula* stable environmental conditions tend to prolong the male phase of these individuals that are suitably mated and sedentary." These points are further illustrated in his diagram, a part of which is reproduced in Figure 46.

There is evidence from the earlier work of other observers, (54, 87) which these recent studies do not entirely replace, that association with a female is important for the full realization of the male con-

dition as well as for its prolongation. With these snails the tendency to become first a male and later a female is probably determined by heredity, although the hereditary mechanism which promotes such a shift is at present unknown. The point of interest for this discussion is that the association

FIG. 46. As *Crepidula fornicata* gets older and larger it passes successively from the sexually immature through the male on into a final female stage. Mated males retain that stage longer than if actively motile. (From Coe.)

with others, especially among mated males, tends to postpone transformation to the opposite sex.

Some cases are known in which the presence of other animals of the same species determines the sex. One of the most thoroughly studied is that of the worm *Bonellia,* (21) in which the sexually undifferentiated larva does not, in nature, become the small parasitic male unless it is associated with the large female.

Among certain nematode worms which are parasitic in insects, if few eggs are introduced into, for example, grasshoppers, (3) most of the resulting

nematode parasites are females; but if many eggs are fed, the nematodes that hatch are almost all males. The results are not to be ascribed to a differential death rate, for approximately 75 per cent of the eggs develop in both cases.

In *Crepidula* and *Bonellia* and nematodes, both males and females are always present in a population, though in differing ratios. In cladocerans, however, of which *Daphnia* is an example, the species may be carried along for many generations by the females alone. They produce eggs which do not require fertilization, but which develop directly into females that again produce other females like themselves. In these cladocerans the race is usually made up of females alone, but at times there is an outbreak of sexuality; males and sexual females appear and the fertilized eggs which result from their union are more resistant to adverse conditions than those which are ordinarily produced and which require no fertilization. These resistant eggs enable the species to survive times of environmental stress, such as winter's ice or the drying-up of the ponds in which these small crustaceans live.

In one species of *Moina,* (5) which has been much studied by the biologists at Brown University, crowding of the females is an effective method of bringing on the outbreak of males and sexual fe-

males, so that overcrowding may be rated as a time of environmental stress. Either by the shortage of food, by the accumulation of waste products, or from some other cause, the association of many female cladocerans together results in the production of eggs which have a different prospective potency from those the same females, uncrowded, would produce; and sexual males and females are the result.

It is evident from these varying examples that even the fundamental matter of sex, with the caste-like divisions of labor that result from two sexes, may be determined by the close association of animals of the same species. There is some reason, though perhaps it is slight, for suggesting as in Chapter III that sex itself may have grown originally out of mutual acceleration in division rates when two or more primitive organisms were in close contact in small space. The whole matter of sex may hark back to some of the basic aspects of mass physiology which were set forth earlier in this book.

Sex in its different aspects plays a highly important role in the social affairs of animals. It is interesting to find that this fundamental cleavage through so much of animal life can at times be controlled by group relationships. Such considerations serve again to emphasize the difficulty of drawing a hard

and fast line, or even a fairly distinct band between social and sub-social living.

One phase of the social implications of sex has escaped general comment. I heard it first mentioned by Professor Wheeler. (123) Apparently when there is a social difference between the sexes it is the females that are the more and the males the less social; and the few striking exceptions only confirm the rule.

Among the social ants, bees and wasps the normal affairs of the colony are carried on by the females. They produce males only when they are needed to fecundate the young virgin females at the time of their nuptial flight. The males contribute nothing to the protection, feeding or housing of the colony; after their one sexual activity they die or are killed off, and the females which are lucky enough to secure a good nesting site carry on with their female offspring until sexual reproduction again becomes the order of the day (Figure 47).

With many of the herds of mammals, the main duties of communal life are borne by the females. They protect and rear the young and herd together to protect each other. The males keep to themselves except during the relatively brief period of the sexual rut. Even when they join the main herds, as in the case of the Scottish red deer, frequently the

males do not fuse with the others. When danger appears during the rut, the stags make off and rejoin the females when it is past. After a male is sexually spent, frequently before the close of the breeding season, he withdraws, and the spent males form stag

FIG. 47. Castes of the common honey-bee; *a*, queen; *b*, male (drone); *c*, worker. (After Phillips.)

parties which are distinctly less social than the bands of females.

In commenting on the relative sociability of the sexes among red deer, Darling says: (38) "Matriarchy makes for gregariousness and family cohesion. The patriarchal group (among deer) can never be large, for however attentively the male may care for his group he is never selfless. Sexual jealousy is always ready to impinge on social relations leading to gregariousness. . . . I contend that the matriarchal system in animal life, being selfless, is a move toward the development of an ethical system."

The flocks of male birds whose social organization we have studied in Chapter VI are more combative than the females. The human male writes the great poems, builds the great bridges, performs the outstanding scientific research; but he is also the criminal, the war-maker, the disturber of the peace. It is the human female that is the highly social force with our species, and in this we are again similar to the others mentioned.

Among the social animals only the termites have fully socialized males; with them the male reproductives consort with the female throughout life. Half the soldiers are males and the other half are females, and so are the workers. Termites are lowly insects, but in this one trait they lead the world. No one knows how the socialization of male termites was brought about, and if we should learn their secret it probably could not be applied directly to human affairs.

When we turn from the far-reaching division of most animals into two sexual castes to explore the origin of the more specialized castes of insects, we find two different essential kinds, the reproductives and the sterile types. With bees, ants and wasps, for example, the usual reproductive females can produce eggs without being fertilized by a spermatozoan. Such eggs always give rise to males. From

the store of sperm which she received in the nuptial flight the same female can allow her eggs to be fertilized; such fertilized eggs become females.

We have seen the comparative unimportance of the males. Although the active colony is usually composed of females only, these may be quite different in appearance and function. Typically there are the reproductive females and the sterile ones. Among the ants the sterile females are divided into the protective soldiers, whose main function is to protect the colony from the attack of other species of animals, and the workers proper. The ant workers are subdivided on the basis of size (Figure 48).

Professor Wheeler made the study of these social insects, particularly the ants, his life work. In a small book, published in 1937 after his death, he reaffirmed his belief that ants and bees have evolved from ancestral wasps, and that each has developed the caste system independently. (124)

With bees and wasps, whether a given fertilized egg is to produce a worker or a sexual "queen," better called a reproductive female, depends on the treatment and food which is given to the grub which hatches from the egg. If she receives plenty of food and is given space in which to grow she becomes fully matured sexually; if fed less and kept more crowded she becomes an incomplete female

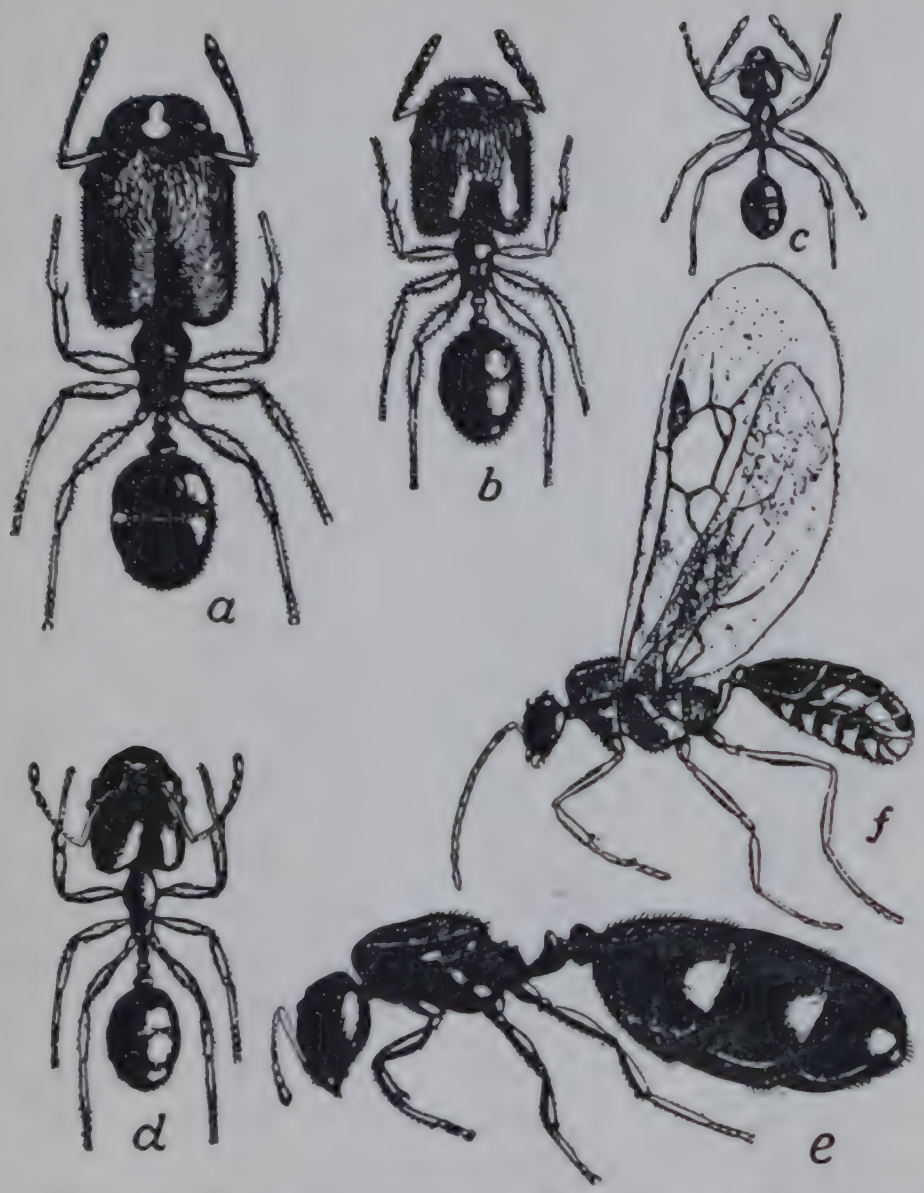


FIG. 48. Some ant castes: *a*, soldier; *b*, form intermediate between soldier and worker; *c*, worker; *d*, form intermediate between soldier and worker; *e*, queen that has shed her wings; *f*, winged male. (After Wheeler.)

and is known as a worker. Apparently the fundamental difference can be brought about only by the treatment which the developing grub receives after hatching, and is not a matter of heredity. Just how the workers are stimulated to give one or more grubs the treatment that will allow them to develop their full reproductive capacities is not fully known. If, however, the queen bee dies or is removed from the colony, workers will start enlarging one or more of the cells which contain developing grubs, change their care and feeding and so allow them to transform into fertile reproductives. Perhaps they are kept from doing so when a queen is present by something like a social hormone, which there is good reason for thinking is produced by the even more social termites.

The mechanism which results in caste formation among ants need not be the same as that in wasps and bees, since it is generally conceded that they had a separate social evolution. For years two theories have been promoted as to how ant castes came into being. One group of students thought that ant castes were determined as were those of bees and wasps, by care and food; another group was equally sure that the differences were hereditary. After confessedly wavering between the two views in his long study of ants, Professor Wheeler in his posthumous

book presents the evidence which finally caused him to decide that with ants the whole matter of caste formation is primarily controlled by heredity.

This is a question which will undoubtedly occupy students of ants for years to come. The evidence is not all in, and the fact that at present it tends to indicate that ant castes are determined by heredity makes all the more interesting the instances in three separate kinds of social insects of the apparent evolution of group control of castes after the hatching of the egg. To this hasty sketch of the operation of group determination of caste in wasps and bees may be added that of termites.

The bees and their allies belong to one of the most specialized of insect orders, so that they are assigned a high position in the evolutionary tree of that class of animals. The termites, miscalled white ants, belong to a relatively unspecialized insect order related to the cockroaches, and stand low in the evolutionary scale among the insects. They have, however, reached a high state of social development.

Unlike bees, ants and wasps, the colony, as we have said, is at all times composed of males and females in approximately equal numbers. There are male and female reproductives of which three different kinds are known; these are the so-called first form which have wings for a time and engage in a

nuptial flight, second form reproductives with wing buds, and third form, which are wingless; and there are the sterile workers and soldiers in which both sexes are also represented equally. The colony is usually composed of reproductives of some one sort, and the two sterile castes (Plate V).

The controversy as to whether caste formation is a result of heredity or of the social environment has been as intense with students of termites as among students of ants. The trend of present information tends to support the theory of control by the environment. (27, 75) A certain California termite called *Zootermopsis* has reproductives and soldiers in its colonies, but no workers in the accepted sense of the term. Their place is taken by the younger nymphs, all of which have the possibility of developing into one of the reproductive grades or into soldiers. When Dr. Castle of the University of California (27) set up experimental colonies of nymphs alone, he obtained in due time one or more pairs of reproductives. If the small experimental colony lacked a fertile male, one of the nymphs developed into that; if a fertile female was lacking and a male was placed in the colony, a nymph developed into a fertile female. If the nymphs in a colony that lacked both males and females were fed on filter-paper which contained an extract of fertile females made with

PLATE V. Winged reproductive caste, soldiers and workers of a termite from British Guiana. This is one of the largest species of termites and is shown life-size. A, winged reproductives; B, soldiers; C, workers. (Photograph by William Beebe.)

alcohol or ether, the males appeared at the usual time, but the females were delayed by twelve or sixteen days on the average.

Ordinarily in *Zootermopsis* only one soldier appears in the first year of the life of the colony. By removing the soldier as soon as it appeared in the experimental colony it was possible to get as many as six soldiers within the time that would ordinarily have yielded only one.

In explanation of these and other similar data Dr. Castle expresses his opinion that at the time of hatching all nymphs possess three sets of possibilities to the same degree; namely, they may become sexually mature though wingless, they may become winged and sexually mature, or they may become soldiers. At some stage these chances are narrowed to two possibilities: the nymph may become sexually mature or it may develop into a sterile soldier. Since the reproductive possibility is present in all nymphs and since its expression is inhibited by a substance produced by a functional reproductive and eaten by the nymphs, the absence of functional reproductives would allow this potential power to express itself. Just what determines that one of the first small lot of eggs will become a soldier is not known, but it can easily be seen that when one soldier has started to develop it too may give off an

inhibiting influence which prevents other nymphs from becoming soldiers. In the normal course of events a second soldier appears only when the colony has become sufficiently numerous so that the soldier-inhibiting substance is spread among so many that the effect on any one nymph is weakened; and something of the same effect of numbers may explain why, in a large colony, many nymphs develop at times into sexually mature and winged forms.

There seems to be a relation to the more generalized situation noted earlier. When many animals are exposed together to a given amount of alcohol or some other toxic material, no one of the many may receive any overdose, as will certainly happen when one or a few individuals meet the full effect of the poison. This type of relatively simple mass effect, first discovered in experiments on group physiology among animals that at the most are only partially socialized, apparently turns out to be an important mechanism in regulating caste formation among these highly social termites; and some similar mechanism may control the activity of worker bees in producing new queens. It is true that the control of caste production is probably not the simplest form of physiological mass action, for the insects may from time to time become less sensitive to such inhibition. At these times, many of the

nymphs may develop into the winged reproductives that swarm forth in the nuptial flight.

As many know, most termites eat wood which, paradoxically enough, they are unable to digest although they do obtain their nourishment from it. The answer to this riddle is that the termites harbor in their alimentary canals several species of flagellate protozoans which can and do change the wood into substances which both termites and these flagellates find highly nutritious.

From many structural relationships we know that termites are close relatives of cockroaches, and studies by Dr. Cleveland of Harvard (34) have shown how the termite societies may have arisen from the much less social cockroaches. Here we have an example of one of the many possible connections between highly developed social life and the less social state illustrated by the mass physiology characteristic of animal aggregations.

Cryptocercus is a wood-eating cockroach which is found in decaying wood of the forests of the Appalachian mountains from Pennsylvania to Georgia, and along the coastal mountains in the northwestern part of the United States. Like their relatives, the termites, these cockroaches feed on wood, and also like the termites they harbor wood-digesting protozoans in their alimentary tract. These wood roaches

and many termites cannot live long if deprived of their associated protozoa, as can be done by appropriate treatment in the laboratory.

The young of both cockroaches and termites hatch out without these essential protozoans. The termites obtain theirs by swallowing a drop of liquid which has just emerged from the anal opening of another termite; the cockroaches get their protozoans by eating the pellets passed from the alimentary tract of molting individuals. Once a cockroach obtains a good supply it renews itself. One such cockroach or a pair can emigrate to a new log and live there for a lifetime. Since, however, adult cockroaches do not molt, the young of such an isolated pair, when hatched, could not receive the so-necessary intestinal protozoa, and hence a pair, if isolated, could not found a new colony. Actually the eggs hatch at just about the time of the annual molting season when the young growing roaches cast their outer covering and a part of the lining of their alimentary tract. At this time the newly hatched young can obtain protozoa readily and thereafter they retain them. The habit of living together is necessary in order that the growing, molting young may transmit their protozoa to the newly hatched nymphs.

The social situation is still more necessary for the termites. With them all the intestinal protozoans are

lost with each molt, and each time that happens each newly molted individual must obtain some of the protozoans from another member of the colony or it will starve. The newly hatched termites often obtain protozoa before they are twenty-four hours old, and an artificially defaunated termite, if allowed to associate with his normal fellows, is reinfected within a few days. With the termites, colony life is an absolute essential and only the winged males and females, the first form reproductives already infected with protozoans before taking the nuptial flight, can even start a colony without the presence of others to carry the needed cultures of protozoans.

Many cockroaches which neither eat wood nor harbor wood-digesting protozoans reproduce so rapidly that given good hiding places and plenty of food they aggregate in large numbers, as many housewives know. These cockroach aggregations, which appear to be formed as a result of tropistic reactions to the environment, accompanied by toleration for the presence of others, permitted the wood-roach *Cryptocercus* to develop the habit of passing protozoa from one individual to another, and so began the long evolution which has resulted in the highly adapted, wood-eating roaches found today.

The same basic adaptation allowed their relatives, the termites, to start on the much longer road they

have traveled to reach their present state of highly developed social life.

We cannot outline the steps taken very closely, but it would seem that in this cockroach-termite stock aggregations allowed aspects of mass physiology to develop which in turn permitted a closely knit and varied social evolution. This is about as near as we have yet been able to come to charting a direct and obvious truly social development from a slightly social or sub-social animal aggregation.

Among grasshoppers crowding can produce obvious structural changes (Figure 49). Certain species of grasshoppers found in semi-arid regions, such as those of South Africa, have two phases (5) that are quite distinct from each other. The phases are sufficiently different so that in the past they have been described as being different species. There is at present much evidence which indicates that the phase *solitaria* can be turned into phase *gregaria* by crowding the young nymphs into dense masses. The opposite transformation may take place when the nymphs of phase *gregaria* are reared under uncrowded conditions. The differences between the two extend into color, form and size.

Similarly plant-lice, which are also called aphids, exist in winged and wingless forms which tend to alternate. When the wingless aphids have approxi-

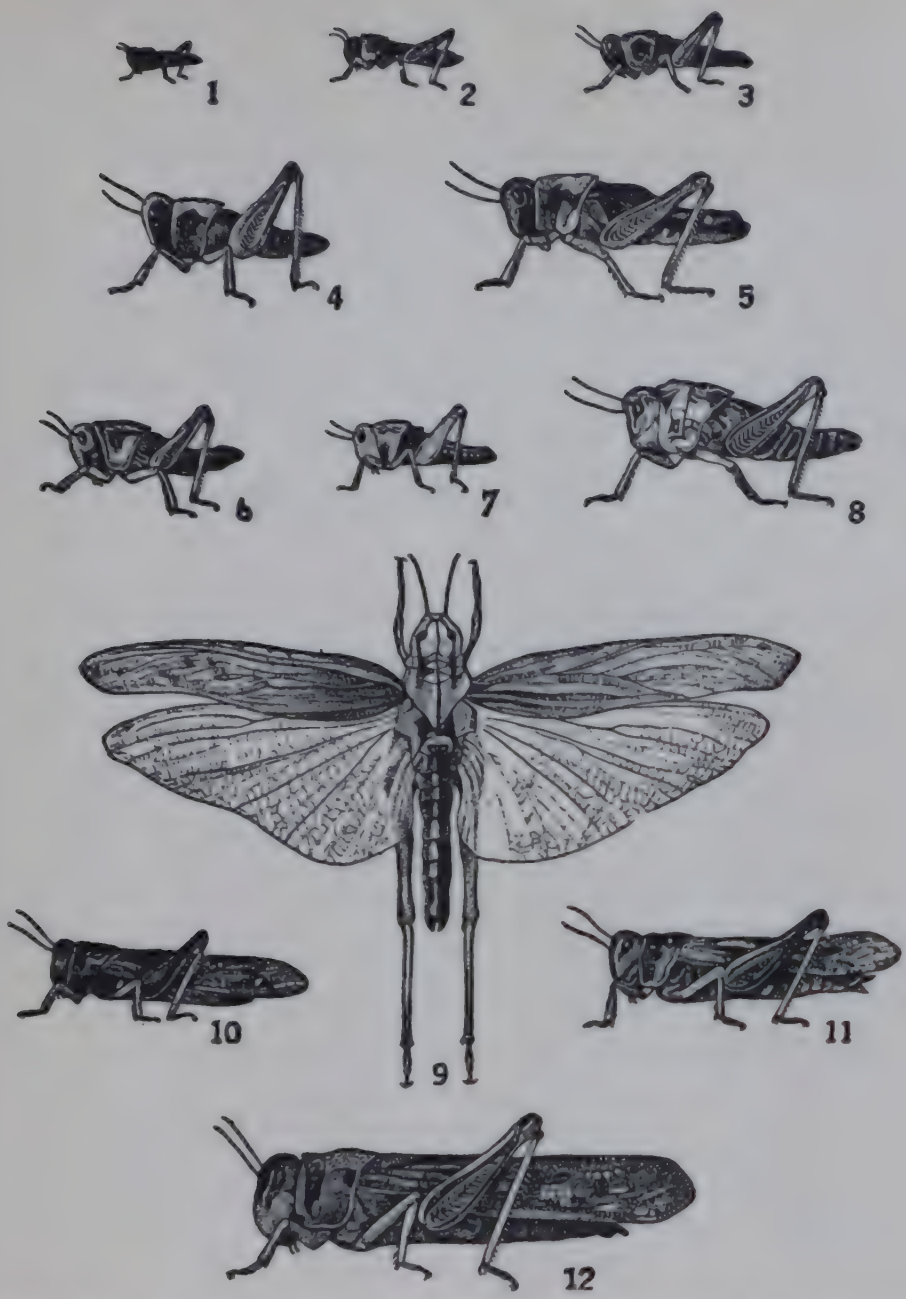


FIG. 49. The five upper nymphs (1-5) and the lowest adult belong to the swarm phase; the others (6-11) show different aspects of the solitary phase of the brown locust (*Locustana pardalina*) of South Africa. This is a black-and-white copy of a color plate by Faure. Black here represents black or bluish-black in the grasshoppers; heavy stippling represents dark brown; light stippling represents light or golden-brown except in parts of Nos. 7 and 9 which are green.

mately exhausted the juices from one food plant the next generation appears with wings; in flying about, some of them will usually find a new and suitable food plant where they can settle and carry on. With some species one of the most effective ways of keeping wings from developing is to isolate the individual aphids and, conversely, one of the best recipes for obtaining winged forms is to allow them to become crowded. (104)

These distinctly different types of grasshoppers and aphids roughly suggest the structural differences between the castes of social insects, just as comparison was suggested between the structural differences of caste and of sex. The resemblance is so close that the line cannot be drawn between its manifestations in social and infrasocial animals. Not only that, but the mechanisms by which the castes are produced appear in many instances to be like those which may occur when animals are aggregated together, even though the aggregations are below the level usually regarded as marking the lower limit of truly social life.

And since no one has yet demonstrated the existence of truly asocial animals it is impossible to define the lower limits of sub-social living. All that can be found is a gradual development of social attributes, suggesting, as has been emphasized throughout this

book, a substratum of social tendencies that extends throughout the entire animal kingdom. From this substratum social life rises by the operation of different mechanisms and with various forms of expression until it reaches its present climax in vertebrates and insects. Always it is based on phases of mass physiology and social biology which taken alone seem to be social by implication only.

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